MALACOLOGICAL REVIEW

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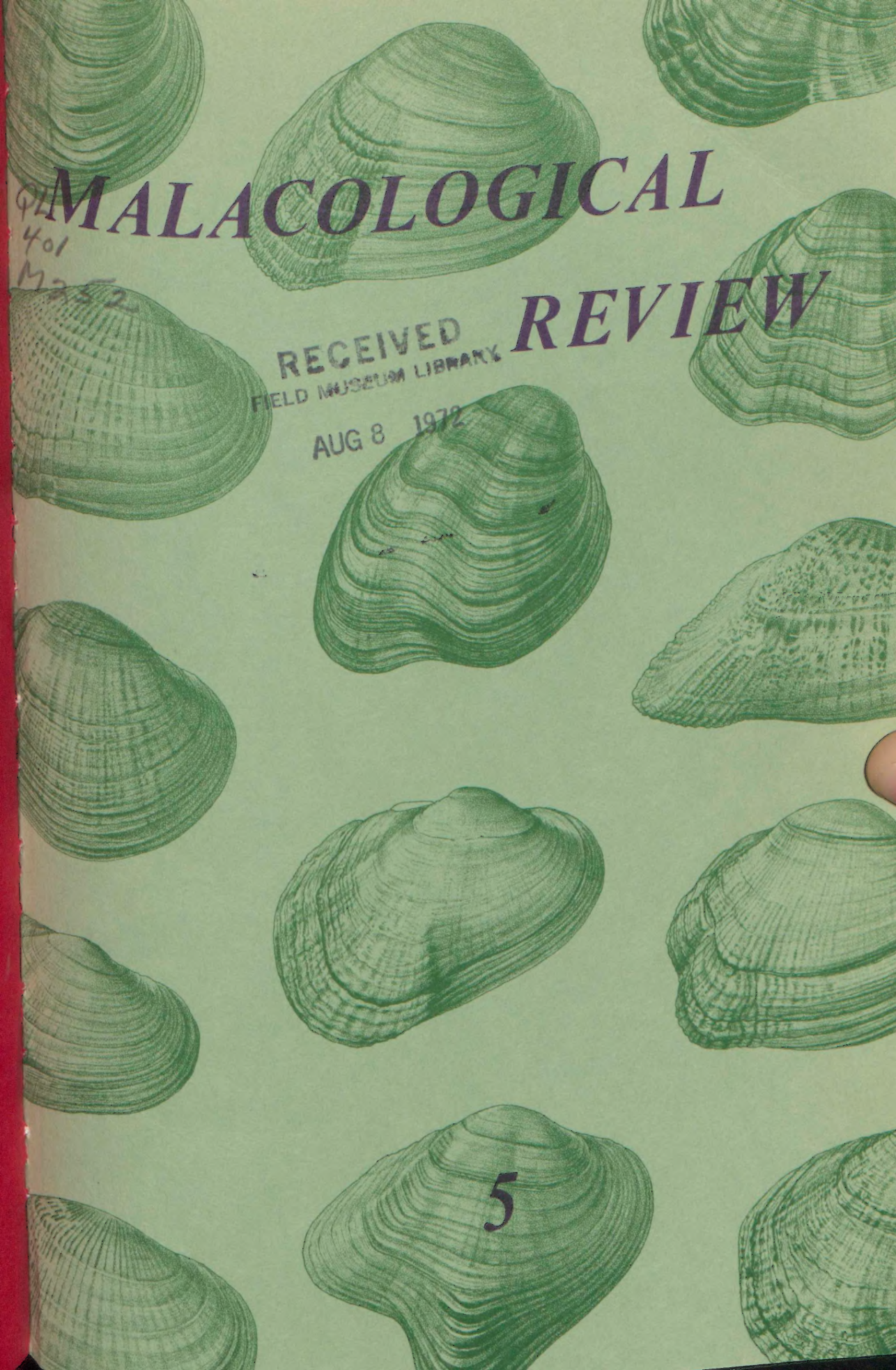

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1972

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1972

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VOLUMES, ISSUES AND PUBLICATION DATES OF *MALACOLOGICAL REVIEW*.— *Malacological Review* was first published in one number for the year 1968. This single issue (187 pages) constituted Volume 1. During each of the years 1969 (Volume 2) and 1970 (Volume 3) two semiannual numbers were published, each two issues for a calendar year constituting a volume. Hereafter we intend to continue publishing two issues a year, each formally designated as a "number". The first issue of each volume henceforth will be "Vol.—, No. 1" and the second issue "Vol.—, No. 2". Occasionally, both issues for a calendar year may be combined and designated as "Vol.—, No. 1-2". Each volume will normally consist of about 200 pages, although this may vary from time to time.

Publication dates of past issues are as follows: Vol. 1, 7 June 1969; Vol. 2 [No. 1], pages 1-102, 10 June 1969; Vol. 2[No. 2], pages 103-214, 8 May 1970; Vol. 3 [No. 1], pages 1-102, 28 May 1970; Vol. 3 [No. 2], pages 103-192, 13 March 1972; Vol. 4 [No. 1], 27 July 1971; Vol. 4, [No. 2], 10 February 1972.

SUPPLEMENT TO *MALACOLOGICAL REVIEW*, VOLUME 5 (1972).— *Malacological Review* will publish a supplement to Volume 5, 1972, which will not be included in the regular subscription price to *Malacological Review*, but can be purchased upon order from our American, Australian or Japanese editorial offices (see inside back cover for addresses). This supplement to Volume 5 is by Gary L. Pace, The University of Michigan, and is entitled *The freshwater mollusks of Taiwan (Formosa)*. This illustrated publication deals with the systematics, ecology, distribution, zoogeography and parasitological relationships of the freshwater gastropod fauna of Taiwan, The Republic of China. The prices of this monograph are US$ 15.00, A$ 13.50 or ¥ 5400.

NEW SUBSCRIPTION PRICE FOR *MALACOLOGICAL REVIEW*. — Beginning with Volume 5 (1972) the subscription price for institutional orders coming directly from North American institutions (i.e., not through a subscription agency), as well as for all foreign institutions and foreign institutional subscriptions through agencies, will be increased from US$ 5.00 to US$ 8.00 (A$ 7.15, Rs. 60.00, ¥ 2560, E£ 3.5). North American institutional subscriptions handled through subscription agencies will be US$ 9.00 (due to the extra handling required in processing orders). Subscription price for private individuals will remain the same for North American subscribers (US$ 5.00), but subscriptions for non-North American private subscribers will be increased to US$ 5.50 (A$ 4.90, Rs. 42.00, ¥ 1760, E£ 2.5) to defray postage costs.

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ERRATUM, Vol. 4, No. 2, p 193: part *a* of couplet 7 of the 'Key to the valid genera and subgenera of Succineidae' should read "Right tentacle assembly passes to the inside of the terminal genitalia... *Quickia*."

BRIEF COMMUNICATIONS

* * * * * * *

THE PODOCYST IN PULMONATE EVOLUTION.(1) — In 1884, Jourdain first used the term "podocyste" for the embryonic extension of the foot of land snails. Earlier observations of the structure were made by Gegenbaur (1851) on *Clausilia* and by Semper (1870-94) on *Partula* and *Achatina*. Jourdain found the podocyst of *Limax agrestis* and *Arion rufus* to be a contractile hollow body of ciliated ectodermal cells covering stellate mesodermal cells within a fluid filled cavity. The alternating contractions and relaxations of the podocyst were observed to circulate the fluids through the embryo creating passive cycles of reduction and distension in the head vesicle. Jourdain felt that the podocyst is primarily respiratory since it is normally flattened against the outer egg membrane in a position advantageous for gas exchange. He also thought that the structure serves for the uptake of the surrounding albumen, the main source of nourishment for the embryo.

Simroth (1912) stated that the albumen of the egg is taken in through the mouth and that the podocyst does not have a nutritional function. He also noted that a podocyst is present in all of the Stylommatophora, except in the Succineidae and in groups now recognized to be opisthobranchs. Simroth additionally said that one stylommatophoran, *"Bulimus"*, lacks a podocyst. This singular exception is based solely on the brief note by Semper (1862), who worked on the embryology of the freshwater prosobranch, *Ampullaria*. Semper only mentioned that *"Bulimus citrinus* Brug." lacks a podocyst, but he failed to give further details, to give any illustrations, or in any way to clarify in what stage and condition his specimens were in, alive or preserved, *etc.* . Apparently *Bulimus citrinus* is actually the camaenid *Amphidromus chloris* Reeve (*fide* J. P. E. Morrison, pers. comm.). No subsequent embryological information is available on any species of the Camaenidae. Since this is the only reference to a stylommatophoran without a podocyst in the literature, we are presently investigating camaenid snails in an effort to evaluate the validity of Semper's observation.

Authors subsequently have de-emphasized the nutritional role of the podocyst because of Simroth's statement that albumen is incorporated only through the mouth. Our observations on a number of species indicate that a large part of albumen ingestion occurs during the period when the mouth is closed from the albumen cells of the digestive system.

Cather (1971) suggested that the podocyst evolved following a reduction of yolk emerging with the subsequent utilization of capsular albumen as the major form of nutrient in an analogous fashion to the embryonic structures specialized for albumnotrophy in the capsular eggs of leeches and oligochaetes. The enormous surface area of the podocyst is almost certainly utilized for respiratory and excretory gas exchange, an exchange made even more efficient by the rhythmic contractions of the podocyst. These functions appear to have evolved concomitantly.

In 1960, Elbers & Bluemink found that there is pinocytotic activity in unspecialized ectodermal cells of the blastula of *Lymnaea*. Bluemink (1967) demonstrated pinocytotic incorporation of electron opaque thorium dioxide (trade name "Thorotrast", Fellows Testagar, Detroit, Michigan) and capsular albumen mixtures by the general surface cells of the *Lymnaea* embryo, at blastula and later stages.

We have investigated the functional morphology of the podocyst at the ultrastructural level with the method of Bluemink, using embryos of *Anguispira alternata* (Fig. 1) and *Partula otahitiana*, both of which have large well developed podocysts. Embryos were removed from their capsules at appropriate stages and placed in a 1:1 mixture of Thorotrast and capsular albumen for specific intervals. These embryos were then rinsed in isotonic saline to remove the adhering albumen and fixed in 2% gluteraldehyde at 4°C for an hour, rinsed in phosphate buffer (pH 7.9) several times, post-fixed in 1% osmium, and dehydrated and embedded in Epon. Sections were stained with uranyl acetate, and examined with an RCA EMU-3 electron microscope.

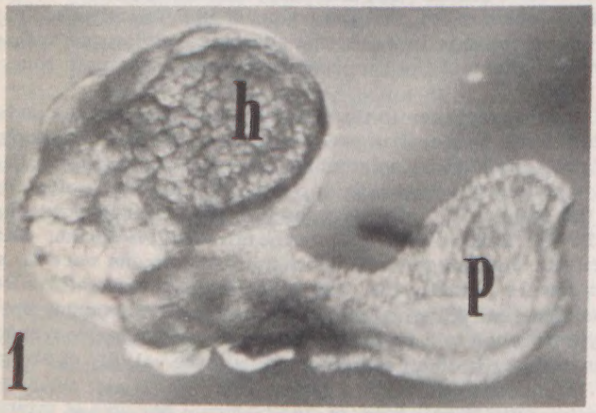
Thorotrast particles were found incorporated within the ectodermal cells of the podocyst in less than an hour of exposure. The cells contained many membranous vesicles surrounding aggregates of Thorotrast (Fig. 3), indicating albumen uptake by pinocytosis. The external surface of the podocyst is not only ciliated, but it has an extensive coat of microvilli. Thus, the ultrastructural detail supports the view that the podocyst is a highly specialized organ and that it has an albumenotrophic function. Other embryonic cells may take up albumen, but lack such specilizations for uptake demonstrated in the podocyst.

We have examined embryos of the ovoviviparous *Partula gibba*, *P. otahitiana* and *Samoana diaphana*, and the oviparous *Cionella lubrica*, *Vallonia pulchella* and *V. costata*, all in the Orthurethra; the oviparous *Stenotrema hirsutum*, *Tridopsis multilineata*, *Helix pomatia*, *Zonitoides nitidus*, *Ventridens ligera*, *Deroceras reticulatum* and *Limax flavus* of the Sigmurethra; and the oviparous *Succinea ovalis* (Fig. 2), *Catinella vermeta* and *Omalonyx felina* in the Heterurethra. All orthurethrans, mesurethrans and sigmurethrans described in the literature and all those examined by us have well developed podocysts. *Succinea putris* (Schmidt, 1895) and the heterurethran species noted above all lack podocysts.

The absence of the podocyst in the albumen-dependent egg of the Succineidae indicates that this group is not closely related to the orthurethrans or sigmurethrans. The contention of Solem (1969) that the succineids are related to the sigmurethran aulacopods, i.e., to the arionids and limacoids, is not supported by the embryological evidence, evidence which we believe to be conservative. The development of aulacopod snails is among the most specialized found in gastropods (Carrick, 1939), while succineids show few

specialized features in their development. It appears unlikely that the highly developed podocyst of the sigmurethrans would have been lost to the extent that there is no vestige of it in the succineids, particularly when albumen is the main source of nourishment in their yolk-poor eggs.

On the basis of morphological features, Rigby (1965) proposed that the Succineidae are most closely related to opisthobranchs, while Cook (1966) and van Mol (1967) considered succineids most closely related to basommatophorans on the basis of their cerebral ganglia. These proposals were critically evaluated by Patterson (1971) and will not be repeated here. In addition, we must point out that the embryonic kidney of succineids appears intermediate in structure to that of basommatophorans and stylommatophoran sigmurethrans (Meisenheimer, 1899) and is unlike that of opisthobranchs.



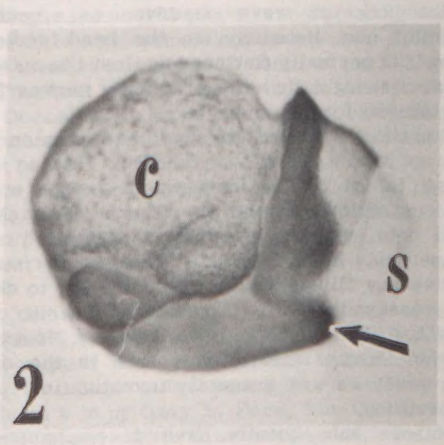


FIG. 1. Embryo of *Anguispira alternata* with a well developed podocyst (p) and head vesicle-visceral hump (h). X 150.

FIG. 2. Embryo of *Succinea ovalis* at a comparable stage, but lacking a podocyst. The pointer indicates the corresponding position of the foot to the podocyst in Fig. 1. Shell (s), cephalic vesicle (c). X200.

FIG. 3. Electron micrograph of podocyst cells of *Anguispira* embryo with free Thorotrast particles (t) and Thorotrast particles within a membranous vesicle (v). X18,000.

We support Patterson's view that the egg mass is unsuitable for systematic analysis due to the great diversity in closely related groups (Jura & George, 1958), and because we believe that many of the observed differences result from the amount of mucus produced. The detailed structure of the egg capsule may be more important generally for showing possible systematic relationships, but in succineids there are no distinctive features which allow discrimination between the groups we are considering here (George & Jura, 1958).

Although embryological evidence is currently inadequate to critically place the succineids' taxonomic position in relation to other gastropod groups, the evidence nevertheless convincingly indicates that succineids are at most only distantly related to orthurethrans and sigmurethrans. The developmental characteristics of those succineids so far investigated could be derived from any proposed ancestral group. But, more detailed investigations, such as those we now have in progress may yield more definitive data for drawing conclusions on the systematic position of the Succineidae.

Embryological examination of several orthurethran species has failed to provide evidence on the origin of their suborder. Development in orthurethrans is highly specialized and essentially identical to that of the sigmurethrans. The ovoviviparous orthurethrans all seem to have well-developed calcified egg shells which disappear as the embryos' shells are formed, just as in the oviparous forms. This indicates a secondary development of ovoviviparity from an egg modified for a terrestrial environment, and further suggests that this development has had a relatively long evolutionary history. Embryological evidence indicates that orthurethran and sigmurethran snails are closely related to each other, but that they have few characteristics in common with heterurethran snails.

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* * * * *

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* * * * *

MUSSELS IN THE UNIQUE NICKAJACK DAM CONSTRUCTION SITE, TENNESSEE RIVER, 1965. — Nickajack Dam is located at Tennessee River Mile (TRM) 424.7 in Marion County, Tennessee, just northwest of the juncture of the state lines of Alabama, Georgia and Tennessee. This dam is about 6.4 mi. below the site of Hales Bar Dam, which it replaced, and below Walden Gorge, which Ortmann (1925) used to separate the mussel faunas of the upper and lower Tennessee River. The mussels discussed here were collected 16 June 1965, the day the coffer dam was dewatered and the riverbed exposed for construction of the dam.

Total drainage above Nickajack Dam includes 21,870 sq. mi. or about 1/2 of the total Tennessee Valley drainage area. Average annual rainfall is 51 in. (129.5 cm). Approximate average annual temperature is 60.8°F (16°C). Average unregulated flow (1875-1965) at Nickajack Dam is 38,000 cfs (Anon., 1969). The Nickajack Dam site lies within a "... narrow zone of interbedded shale and limestone of the Rockwood formation" (Anon., 1963). Bedrock at the site is overlain by an average 30 ft. of alluvia. The riverbed is rock for the most part. "The strike is N 40°E, essentially at right angles to the river, and the dip is 2° to 3° upstream." The Rockwood is the principal geologic formation on which the dam is situated. The Rockwood formation of Silurian age is about 120 ft. thick at the dam site. The Sequatchie formation, underlying the Rockwood, is approximately 235 ft. thick (Anon., 1963).

The No. 1 coffer dam at the Nickajack Dam construction site was dewatered on 16 June 1965 (Fig. 1). Since the entire cross section of the river at the site was dewatered, a unique opportunity for collecting mussels was provided. The normal streamflow was diverted to an artificial channel around the construction site; this made it possible to collect specimens from the entire riverbed (about 600 ft. wide, 1100 ft. long) within the coffer dam by simply walking over the area. Figs. 2-7 show the configuration of the riverbed.

Seventeen species of mussels and the Asiatic clam (*Corbicula manilensis*) were collected from the site. Seventy-six percent (13 of 17) of the mussel species collected were those reported by Ortmann (1925) in

TABLE 1. Mussel records for the Nickajack Dam site, Tennessee River Mile (TRM) 424.7, 16 June 1965, Scruggs (1960 TRM 384, and Ortmann (1925), Bridgeport, Alabama, near TRM 415. Numerals refer to numbers of specimens collected; "X" indicates that the particular species was present.

Species	Year of collection			
	1965		1960	1925
	Live	Shells only		
Fusconaia ebena			X	
Megalonaias gigantea	10	5	X	
Amblema (costata) plicata		7	X	
Quadrula pustulosa	13	2	X	X
Q. fragosa			X	
Q. metanevra	5	3	X	X
Q. cylindrica				X
Tritogonia verrucosa		2	X	X
Cyclonaias tuberculata granifera		2	X	X
Plethobasus cooperianus			X	X
P. cyphus			X	
Lexingtonia dollabelloides				X
Pleurobema cordatum	12	2	X	X
P. cordatum plenum				X
P. cordatum pyramidatum				X
Elliptio crassidens		5	X	X
E. dilatatus	3			X
Ptychobranchus fasciolaris				X
Obliquaria reflexa		6	X	X
Dromus dromas				X
Cyprogenia irrorata		1		X
Obovaria olivaria				X
O. retusa				X
Actionanaias carinata gibba				X
Plagiola lineolata	1	7	X	X
Truncilla donaciformis			X	
Leptodea fragilis	9			X
Proptera alata	13	1		
Ligumia recta latissima	1	4		X
Lampsilis ovata	1	2		X
L. orbiculata	3	1		
L. fasciola				X
Dysnomia triquetra				X
Corbicula manilensis	12			

FIG. 1. Overall view of the Nickajack Dam construction site. TVA photograph.

FIGS. 2-5. Nickajack Dam construction site. FIG. 2. View of the left side of the dewatered Tennessee riverbed at the construction site, 16 June 1965. FIG. 3. Riverbed configuration at about middle of river looking southeast. FIG. 4. Riverbed configuration showing rubble. FIG. 5. Riverbed configuration showing large boulder in background and erosion sediment in foreground.

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FIGS. 6 and 7. Nickajack Dam construction site. FIG. 6. View of undulating riverbed configuration. FIG. 7. Looking north from the upstream coffer dam. Note abandoned mussel boat in foreground and footprints in erosion sediment. Photographs by author.

FIG. 8. View of the completed Nickajack Dam and Nickajack Reservoir. TVA photograph.

the area of Tennessee River Mile (TRM) 415, Table 1. These were included in Isom (1969) without discussion. The author's data in Table 1 are the result of a random collection that, it is hoped, includes all the species at the collection site, but that represents only a minor portion of the total number of specimens present. Scruggs (1960) reported 15 species of mussels from TRM 384, which is well downstream from the Nickajack Dam site, but still within the Guntersville Reservoir complex of which the Nickajack Dam site was a part before the dam was constructed.

Species noted in Table 1 constitute all of the records that could be found relating to the recent mussel fauna immediately below Walden Gorge. There may be some information on mussels from excavations at Russell Cave National Monument near Bridgeport, Alabama, that would give further insight into the historical fauna of this region.

It is conjectured that a number of the mussels reported by Scruggs (1960) and the author will establish viable populations in the reach below the completed Nickajack Dam (Fig. 8). There are numerous small populations in Guntersville Reservoir downstream of Nickajack Dam that are the basis of this conjecture (Isom, 1969; pers. observ.). There are also numerous species of mussels below Guntersville Dam which may be of value in natural establishment of these species by way of migration of their fish hosts.

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NAMES FOR TWO POLYPLOID SPECIES OF AFRICAN *BULINUS* (BASOMMATOPHORA: PLANORBIDAE). — In a series of publications since 1960, I have shown that the African genus *Bulinus* is remarkable in that it contains a series of polyploid populations or species whose individuals are characterized by exact multiples of the basic chromosome number (x=18) of the family Planorbidae to which they belong. Thereby, *Bulinus* is one of the most cytologically interesting taxon in the animal kingdom. Some species have the normal diploid chromosome number, whereas other species are tetraploid (n=36, 2n=72), hexaploid (n=54, 2n=108) or octoploid (n=72, 2n=144). All of the polyploids occur in the subgenus *Isidora* (=*Bulinus* s.s. in past usage).

Normal diploid species (such as *B. natalensis* and *B. tropicus*) are apparently the only *Isidora* species in South Africa and Rhodesia, and they are also found in the same regions as tetraploids in some areas of West and East Africa south of the Sahara (Senegal, Ethiopia and Tanzania). The tetraploid species *Bulinus truncatus* is the dominant (only?) *Isidora* species occurring in the Mediterranean region, the Near East and Africa north of the Sahara. Other nominal species and subspecies that are also tetraploid (*B. truncatus rohlfsi*, *B. coulboisi*, *B. guernei*, *B. schackoi* and *B. sericinus*) occur south of the Sahara in West and East Africa (Gambia, Ghana, Ethiopia and Tanzania) and in Aden across the Red Sea. Their distribution overlaps that of the diploids in Ethiopia and Tanzania. Hexaploid species are known to occur only in Ethiopia, and octoploid species occur in Ethiopia and possibly in Aden as well. Neither of the latter 2 polyploid forms have scientific names. The information summarized above has been published in a series of papers from this laboratory (Burch, 1960, 1963, 1964, 1965, 1967a, b, 1969; Burch & Huber, 1966; Burch & Lindsay, 1970, 1971; Burch & Natarajan, 1966; Natarajan, Burch & Gismann, 1965; Wu, 1971) and in Brown, Schutte, Burch & Natarajan (1967) and Brown & Burch (1967).

Although the 2 higher polyploids do not have formal scientific names, it seems quite evident that they are distinct species in the biological sense. Firstly, they have more than single isolated occurrences, the hexaploid being known from 4 localities in Ethiopia and the octoploid has been found in 6 localities in Ethiopia, and it also apparently occurs in west Aden (Burch, 1964). Therefore, the various levels of organization (cells, tissues, organs, organism) within the polyploid populations are adjusted to the greatly increased numbers of chromosomes, and the various existing genomes are compatible to the environments in which they live. Secondly, populations exhibiting different degrees of polyploidy are reproductively isolated, as we have postulated for some time (Burch, 1965; Burch & Huber, 1965; Burch, 1967a) and which now has been demonstrated by cross-breeding experiments (Wu, 1971). Copulation occurred readily in Wu's experiments, but viable offspring usually were not produced between the diploid and polyploid snails, and in the rare event of successful hybridization, the hybrids were infertile.

The purpose of this paper is to incorporate the 2 unnamed polyploid species, i.e., the hexaploid and the octoploid, into our system of binomial nomenclature.

Bulinus (Isidora) hexaploidus, n.sp.

Fig. 1a

Holotype: UMMZ 231586; Paratypes: 231587

Type locality: Sulultu "River," 15 miles north of Addis Ababa, Ethiopia along the Debra Marcos Road. This is a small permanent stream 2-4 feet wide and 1-2 feet deep. Snails were collected from aquatic

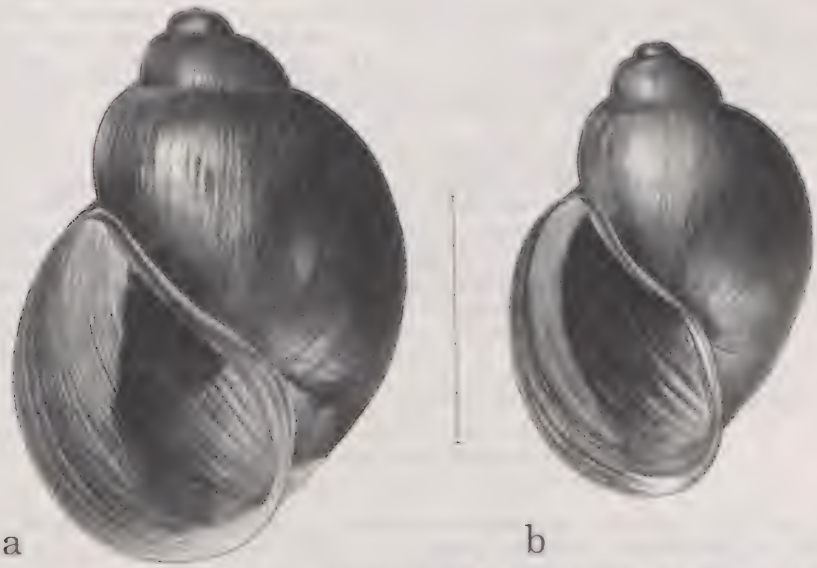

FIG. 1. Shells of 2 new species of *Bulinus* (*Isidora*). a, *B. hexaploidus*; b, *B. octoploidus*. Scale in mm.

vegetation and various other submerged objects.

Description: As their name implies, these snails are hexaploid (n=54, 2n=108). Adult field-collected shells were 9-13 mm high (holotype =10.9mm). They are medium- to high-spired, fragile, transparent or translucent, clear or pale horn-colored. The umbilical opening is sometimes nearly covered over by the columellar margin, but more often it appears as a well-defined opening. The surface of shells cleaned in sodium hypochlorite, as seen by transmitted light at magnifications of 40X or more, is generally smooth, but with growth lines or wrinkles of varying and irregular prominence. At a magnification of 400X the wrinkles at some areas possibly may be interpreted as nearly obsolete riblets, quite irregularly spaced, varying from 0.25-0.75 mm apart.

A notable difference between the animals of this population and the octoploid species described below is the darker colored body and the occurrence of pigmentation on the mantle.

More detailed analyses of the shells and animals of this population of *Bulinus hexaploidus*, as well as descriptions of radulae and soft anatomy, may be found in Wu (1971).

Bulinus (Isidora) octoploidus, n.sp.

Fig. 1b

Holotype: UMMZ 231588; Paratypes: 231589

Type locality: Small body of water 4 km. south of Sheno (Shano) near the Debra Berhan Road, Ethiopia, at about about 9285 feet above mean sea level.

Description: As their name implies, these snails are octoploid (n=72, 2n=144). Adult field collected snails were 8-10 mm high (holotype = 9.2 mm). They are medium- to high-spired, fragile, transparent or translucent, clear to pale horn-colored. The umbilicus is usually nearly covered over by the columellar margin of the aperture. The surface of shells cleaned in sodium hypoclorite, as seen by transmitted light at magnifications of 40X or more, is generally smooth, but with growth lines or wrinkles of varying and irregular prominence. Riblets or other regularly spaced surface sculpturing prominent enough to warrent noticing on the body whorl, even at magnifications up to 400X, are absent.

The animals of this population lack the pigmentation mentioned above for *B. hexaploidus*.

More detailed analyses of the shells and animals of this population, as well as descriptions of radulae and soft anatomy, may be found in Wu (1971).

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MOLLUSK SEMINAR
ANN ARBOR, MICHIGAN
6 August 1971

(Proceedings of *The Society for Experimental and Descriptive Malacology*, 1971)

OPENING REMARKS

J. B. Burch

The American midwest traditionally has been a training ground for North American biologists specializing in the study of mollusks, and the many illustrious scientists and natural historians from this region who have contributed to the advancement of knowledge on mollusks is too long and too well-known to repeat here. The list goes as far back as Rafinesque and Thomas Say, and continues to the present generation of North American malacologists, many of whom were trained partly or wholly in the midwest.

Yet, except for an occasional visit to the annual meetings of the American Malacological Union, or the chance meeting at gatherings of broader scientific societies, biologists working with mollusks in this region have little opportunity to meet and to discuss their research interests, or to contribute to the cross-fertilization of ideas so beneficial to progress in the advancement of scientific knowledge.

So, this year, in the course of discussing the impracticality of travelling some 1200 miles for a meeting on mollusks, held in very expensive surroundings, and mainly among shell-collectors with little or no scientific interest, we decided that it might be beneficial to those in our region to hold a modest meeting to enhance open communication among biologists whose common interest is their choice of research animal, a mollusk.

PROGRAM

Problems in culturing snail intermediate hosts, HENRY VAN DER SCHALIE

The effect of water quality on laboratory culturing of *Biomphalaria pfeifferi* and *Bulinus globosus*, YUNG-SAN LIANG

Seasonal migrations and other movements in Douglas Lake pulmonate snails, PHILIP P. CLAMPITT

Feeding behavior of three species of succineid snails, AMY L. SHRADER

The program in Mollusca at the Ohio State University Museum of Zoology, DAVID STANSBERY

Breeding experiments in the *Bulinus tropicus/natalensis* complex, SHI-KUEI WU

The susceptibility of *Pomatiopsis lapidaria* and various races of *Oncomelania hupensis* to *Paragonimus westermani* and *P. ohirai*, PHILIP T. LOVERDE and KAZUO YASUROKA

Effects of snail tissue extracts on immobilization of schistosome miracidia, YUKIO HOSAKA

A simple macroscopic method of determining crystalline forms of deposited calcium carbonate in mollusc shells by infrared spectral analysis, EDWARD L. COMPERE, Jr. and JOHN M. BATES

The systematic position of *"Lymnaea" bulimoides*, J. B. BURCH and GENE K. LINDSAY

The succineid genus *Quickia*, C. M. PATTERSON

Archaic land snails of the Pacific islands, YOSHIO KONDO and J. B. BURCH

Possible family distribution patterns in pulmonate gastropods, GEORGE A. TE

Developmental regulation of the trochophore of *Nassarius*, JAMES N. CATHER

Of shells and time, AURÈLE LaROCQUE

ABSTRACTS OF PAPERS

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PROBLEMS IN CULTURING SNAIL INTERMEDIATE HOSTS

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Abstract

Our work on snail intermediate hosts of trematode parasites is financed largely by grants. At present these grant-supported programs are mainly as follows: (1) A National Institutes of Health Training Grant in "Medical Malacology" that supports 4 graduate students in studies leading to a doctorate degree; (2) an Armed Forces Epidemiological Board program supported through the Commission on Parasitic Diseases and designed to develop efficient methods for maintaining intermediate host snails for basic studies in chemotherapy, snail control, etc.; (3) a biological supply program supported by the National Institutes of Health in which 5 strains of the 3 human schistosome species are maintained; (4) schistosome dermatitis ("swimmer's itch") studies supported at a low level by several agencies but needing much more intensive study than hitherto possible, since too little is known about the biology of the dozen or more non-human schistosomes responsible for this infestation in the Great Lakes region; and (5) heat pollution studies supported by the Federal Water Pollution Control Administration in which several freshwater pulmonates and one freshwater prosobranch are maintained between 6°C and 34°C to measure both growth and reproduction within that wide range of temperatures. Other programs have been fostered and some are pending, but those listed above comprise a large share of our activities on host snails.

In the course of working on this broad range of programs in which the culture and maintenance of stocks is essential, some basic patterns exist relating to difficulties inherent in providing the kinds and numbers of snails necessary for parasite infection. One of the difficulties concerns the problems of stunting and the accompanying loss in egg-laying capacity that occurs when snails are cultured under crowded conditions. These problems are not new, but were discovered over 100 years ago. While stunting recently has been studied by several investigators, the mechanism responsible for stunting is still poorly understood. Recent studies in our laboratory by Yung-San Liang on both *Biomphalaria pfeifferi* (the intermediate host of *Schistosoma mansoni* in Africa) and *Bulinus globosus* (one of the intermediate hosts of *Schistosoma haematobium*) have provided methods that will enable culturing those snails at a high level of growth and reproduction.

In studies involving *Oncomelania* species (the intermediate hosts of *Schistosoma japonicum*) it is now possible, through the efforts of John French, to produce large numbers of young (at least 500 per month) of each of 5 *Oncomelania* strains. The prepatent period of *S. japonicum* in these snail hosts is 3 months. The susceptibility of the *Oncomelania* species to the various strains (Japanese, Formosan, Chinese and Philippine) of *S. japonicum* is relatively low, often not above 20-40%. If, in addition to this low incidence of the parasite in the snails, the losses of snails that occur during the 3-month prepatent maintenance period are considered, the chances for retaining an adequate supply of parasites are sometimes quite unpredictable. While these problems have now been partially solved, the difficulties that attend the "shedding" of cercariae from infected snails still remain.

To obtain an adequate number of mature cercariae in the laboratory from infected *Oncomelania* it is necessary to crush the snails, although the same snails will "shed" their cercariae naturally over an extended period of time. Efforts are now being made to find what factors are most important for "shedding" cercariae from *Oncomelania*. In studies already undertaken several factors such as light, drying, temperature, periodicity and time of submergence have been tested. In one such test appreciable numbers of cercariae of *O. hupensis chiui* did not appear until 8 hrs. following submergence in water and the total shed took nearly 17 hrs. This same method failed when another species of *Oncomelania* was tested in the same way. While it is most important for work involving the maintenance of cycles of *Schistosoma japonicum* to be able to shed snails without crushing them, there is, as yet, no entirely suitable way to obtain adequate numbers of cercariae other than crushing the snail host.

An important but little understood factor in the maintenance of trematode parasites in snails is susceptibility of the snail in relation to its age at the time of exposure to infective miracidia. My former professor, the late Dr. George R. LaRue, was extremely critical of anyone who claimed that a certain snail was not the host of a particular trematode parasite *if* the exposures were made to anything but *young* snails. In the experience of many other parasitologists the principle that it is better to expose young snails to miracidia rather than adult ones is sound. However, it is often not possible to test any but adult snails because young are not available. In the culture work under way in our laboratory there are a number of cycles maintained in a routine way, and with the availability of this wide range of age-class material, tests are being conducted to determine the relative differences in susceptibility of the different age groups of several *Oncomelania* species to strains of *Schistosoma japonicum*. So far, these studies have demonstrated a large difference in the susceptibility of *O. hupensis formosana* to the zoonotic strain of *S. japonicum* from Formosa when older rather than younger snails were exposed to miracidia. The difference in susceptibility in one series of exposures was as high as 50%. Most of the old snails could not be infected.

THE EFFECT OF WATER QUALITY ON LABORATORY CULTURING OF *BIOMPHALARIA PFEIFFERI* AND *BULINUS GLOBOSUS* [1]

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Abstract

Reports involving the successful laboratory culture of snails are difficult to find, and there has been a great need for careful appraisal of the conditions necessary for laboratory maintenance of some of the more medically important species. In the present studies, the planorbid snails, *Biomphalaria pfeifferi* from Liberia and *Bulinus globosus* from Rhodesia were used.

Commercial green plastic trays (3 x 8 x 12 inches) designed for plant seedlings were employed as aquaria. To each of these was added 1500 ml of water, either glass distilled water, aerated tap water or spring water, as well as a mound of mud on which there was a mixture of 3-wk. old blue-green algae and lettuce. Newly hatched snails were introduced into the trays, 5 snails per tray. The trays were then placed under continuous illumination from 40 watt "cool-white" fluorescent tubes at 25°C to 27°C. At the end of the 2nd week, snails were collected for measurement of their body length, and then placed back into freshly prepared trays. These measurements were performed weekly thereafter (and snails placed into new trays) until the end of the 33rd week for *Biomphalaria pfeifferi*, and the 44th week for *Bulinus globosus*. The numbers of egg-masses and the numbers of eggs were recorded according to the sites on which they were laid. The results were as follows. (1) The kinds of water *per se* had no significant influence on growth (body length) of the snails; (2) Fecundity was adversely affected by spring water. The numbers of eggs laid per *Biomphalaria pfeifferi* snail in trays with glass distilled water, aerated tap water and spring water were 4688, 5454 and 3792 respectively. The numbers of eggs laid per *Bulinus globosus* were 4528, 3452 and 2202 respectively; (3) Sites of egg-laying (either on the containers, under lettuce, or on snail shells) were correlated with the kinds of water used. The percentage of eggs laid on containers by *Biomphalaria pfeifferi* in trays with glass distilled water, aerated tap water and spring water were 65.1%, 40.1% and 29.5% respectively. The figures were 67.4%, 50.9%, and 28.9% respectively for *Bulinus globosus*.

In the next experiments in which the aquaria were set up as described above, the effect of calcium and magnesium ions, which were in large quantity in spring water, were studied. Newly hatched snails were placed into trays as usual, except that the kinds of water used were different. The waters were prepared in such a way that the concentrations of calcium and magnesium ions in these waters would be approximately the same as those found in spring water. That is, in the calcium water there were 128.5 mg/l of calcium ions, in the magnesium water there were 37.9 mg/l of magnesium ions, and in the calcium + magnesium water there were 128.5 mg/l of calcium ions and 37.9 mg/l of magnesium ions. Glass distilled water and spring water served as controls. The results for the period of 16 weeks were as follows. (1) The effect of calcium and magnesium ions on body growth was not observed; (2) Fecundity was adversely affected by calcium ions. The effect of magnesium ions was not observed. The numbers of eggs laid per *Biomphalaria pfeifferi* snail in trays with glass distilled water, spring water, calcium water, magnesium water, and calcium+magnesium water were 1565, 1438, 639, 1859 and 1663 respectively. The numbers of eggs laid per *Bulinus globosus* snail were 1025, 778, 685, 1081 and 895 respectively; (3) Sites of egg-laying were also affected by calcium ions. The percentage of eggs laid on containers by *Biomphalaria pfeifferi* snails in trays with glass distilled water, spring water, calcium water, magnesium water, and calcium+magnesium water were 52.4%, 28.6%, 12.9%, 55.3% and 51.3% respectively. The figures were 47.9%, 5.8%, 29.0%, 51.9% and 14.7% respectively for *Bulinus globosus*.

[1]This work was carried out under the sponsorship of the Commission on Parasitic Diseases, Armed Forces Epidemiological Board and was supported by the Office of The Surgeon General, Department of the Army.

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SEASONAL MIGRATIONS AND OTHER MOVEMENTS IN DOUGLAS LAKE PULMONATE SNAILS

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Abstract

This report describes part of the research - in progress since 1969 at the University of Michigan Biological Station - on the ecology, life history and behavior of 5 species of Douglas Lake pulmonate snails. It is hoped that this study will give more complete answers to such questions as: (1) Do pulmonate snails in lakes undergo seasonal migratory movements, as Cheatum (1934, *Trans. Amer. microsc. Soc.*, 53:

348-407) and others have reported? (2) If so, (a) are such migrations more characteristic of some species than of others? (b) At what time during the season do the major migratory movements take place, and how fast do the snails move? (c) How do these movements correlate with life history changes and density changes through the season? (d) What triggers these movements?

To provide answers to some of these questions, extensive quantitative sampling was done monthly, between April and November, along selected transects from shore to maximum depths positive for snails. Changes in density and life history data - including shell lengths - were recorded. At least 10 m^2 were sampled per station along each transect. Sampling was done directly by hand, aided by use of mask and snorkel, and by SCUBA where necessary.

A clear seasonal migratory pattern is evident in *Physa integra* Haldeman. Along the west shore of South Fishtail Bay in Douglas Lake, in late April and early May after the winter ice melts, adult *P. integra* migrate from scattered localities on a sandy shoal, 25 m wide, toward a substratum of cobbles adjacent to the water's edge, where they reach densities of 15 to 20 snails per m^2 by May 15. They lay their eggs on these stones, and gradually die off during June and early July, being replaced by a rapidly growing new generation. In late August and early September, the juvenile population begins moving away from the cobble shore to a sand substratum 10 to 20 m off-shore, in water about 1 m deep. By mid-November the snails have again become widely scattered over the shoal area, and apparently remain so during the winter months. Few snails move beyond the "drop-off", beginning at 2 m depth, 30 m from shore. Movement toward shore again occurs in spring, completing the migratory cycle.

Helisoma antrosa (=*anceps*) *percarinata* (Walker), however, does not show a seasonal migratory pattern. Along the west shore of South Fishtail Bay, in May 1970, the greatest densities of adult snails were found on a sand substratum between 20 and 30 m from shore, in water 1.0 to 1.6 m deep. The snails deposited their eggs here - often on the shells of other living snails - and suffered almost complete mortality by early July. The new generation of snails did not become clearly evident until August; by September, these juveniles showed the greatest densities - up to 20 per m^2 - in the same area where the parent generation had been found in May. In November, members of this species were difficult to locate, having apparently burrowed into the substratum, but they were present - again in the same area as before - in densities up to 10 per m^2 in May 1971. Lack of evidence of seasonal migratory pattern in this species was similarly shown in other areas in Douglas Lake.

Rates and directions of movement, and factors stimulating movement, were tested by means of field and laboratory experiments during the summer of 1971. Adults of *P. integra*, *P. parkeri* "Currier" DeCamp, *H. antrosa*, and *H. campanulata* (Say), marked and released in the lake in water 3 m deep on a moderate slope, showed preponderant movement up the slope. The 2 *Physa* species moved much more rapidly than did the *Helisoma* species - 7 to 8 m, compared with less than 3 m maximum, in a 24-hour period. Juvenile *P. parkeri*, on a level sand substratum in water 1.3 m deep, dispersed much more rapidly during daylight hours than at night - up to 4 m, as compared to less than 0.5 m maximum, in 10 hours. When given a "choice" between light and darkened areas in a laboratory chamber, both *Physa* species and *H. antrosa* tended to move into, and remain in, the lighted zones; *H. campanulata*, in contrast, showed a slight "preference" for the darkened zones. *H. antrosa*, when placed in a lighted or a darkened chamber over a sand substratum, burrowed into the sand to a significantly greater extent in the lighted chamber. Orientation and movement of the several species in the presence of a current are now being tested. The ecological significance of these and other responses, and their relationship to seasonal migratory movements, are being explored.

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FEEDING BEHAVIOR OF THREE SPECIES OF SUCCINEID SNAILS[1]

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Abstract

Three species of succineid snails, *Succinea ovalis*, *Oxyloma retusa* and *Catinella vermeta*, are found in southern Michigan. Kagan (1952, *Trans. Amer. microsc. Soc.*, 71: 20-44.) mentions that some workers believe that each of these species occupies a definite ecological niche related chiefly to the degree of moisture. *S. ovalis* seems to inhabit rather dry places, *C. vermeta* intermediate ones and *O. retusa* wet habitats. However populations of all 3 species are found within a few feet of one another while all are tolerant to moisture (or sensitive to desiccation), *Oxyloma* seems to be able to venture but only a short distance from water, if at all. If these 3 related species are found in similar habitats, would possible differences in their moisture tolerance be reflected in different foods ingested? Are the snails eating those food types available in slightly different microhabitats?

[1]Supported (in part) by a grant from the National Science Foundation, GB-25986, to Dr. N. G. Hairston, The University of Michigan, for research in Systematic and Evolutionary Biology.

The central problem was to find out exactly what these species of snails eat and to compare the food "preferences" of each species to see if that implied anything about its ecological niche. During June 1971, groups of each species were collected from 5 separate habitats (15 samples of snails from 9 sites in southern Michigan). The snails were identified and samples of their feces and gut contents were placed in water or preserved in 70% ethyl alcohol. The samples were examined and analysed by 3 mycologists from the University of Michigan Herbarium. Special problems with pollen and diotoms were referred to specialists in the Great Lakes Research Institute of The University of Michigan and to Dr. Gary Collins of the Ohio State University Department of Botany.

All 3 species seem to ingest what is available - parts of living and dead vascular plants that occur on land and near water, as well as the fungi associated with their habitats. Yet, the 3 species' feeding habits do seem to reflect slight differences in microhabitat. *O. retusa*, the most water tolerant species, consumed more pollen than the other 2 species, perhaps because it occurred near a water tolerant plant (*Typha*) that produces a great deal of pollen during June. But, it also consumed more green and blue-gree algae than the other species. Those *Catinella vermeta* and *Succinea ovalis* found in very moist habitats had been eating green algae, like *Oxyloma*.

At only one site, the banks of the Huron River, did the species occur together. The foods ingested at this site were quite similar for all 3 species. However, differences in food preferences began to appear when the data from all sites were compared. The case of diatoms is the most interesting. The same snail species seemed to be picking up similar diatoms in similar habitats; but different species did not seem to ingest the same diatoms in similar habitats. *Catinella vermeta* ate more diatoms and more types of diatoms than the other 2 species. This may mean that it traverses more microhabitats, the entire range from shallow water to mud flats to moist shady meadows. It may have more adaptability and a wider niche breadth.

* * *

THE PROGRAM IN MOLLUSCA AT THE OHIO STATE UNIVERSITY MUSEUM OF ZOOLOGY

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Abstract

The basic objective and orientation of the Ohio State Museum mollusk program is the understanding of the process and products of evolution in the Mollusca. Particular attention is given to the species and subspecies levels, with an emphasis on both descriptive and experimental approaches. Since the present curatorial staff has a deep interest and extensive training and experience in aquatic ecology, and since natural selection is a process of organism-environment interaction, it is not surprising that the research projects are designed from an ecological point of view.

Every reasonable effort is made to devote time and knowledge to the very important task of preserving at least a few streams supporting the remaining populations of the uniquely rich North American freshwater fauna. Coordinated with these efforts is the allocation of a major part of our resources to the collection of statistically significant samples of specimens from populations doomed to extirpation, if not extinction, as a result of current dam construction and stream channelization projects, as well as agricultural siltation and other forms of pollution. We invite and encourage our sister institutions to share our efforts along these lines, commensurate with their resources, so that the wealth of biological variability in our native molluscan fauna may be preserved for future generations.

* * *

BREEDING EXPERIMENTS IN THE *BULINUS TROPICUS/NATALENSIS* COMPLEX[1]

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Abstract

An albino strain (without eye pigmentation) of *Bulinus tropicus* from Onderstepoort, Transvaal, South Africa was crossed with pigmented snails (having eye pigmentation) of each of the following 3 populations: *B. tropicus* from Malelane, Transvaal, South Africa; *B. natalensis* from Lake Sibaya, Natal, South Africa; and *B. tropicus* from Lake Baharshangi, Ethiopia. In general, only the eye-pigmentation character was used as a genetic marker. In crosses between the albino *B. tropicus* and pigmented *B. natalensis*, shell characters were also used.

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In 2 breeding experiments with 2 albino and 2 pigmented South African *Bulinus tropicus*, both albino and eye-pigmented parents produced only eye-pigmented F_1 progeny. The eye-pigmented and albino characters segregated in the expected 3:1 ratio in the F_2 generation (produced by brother-sister crosses of F_1 progeny), and in the expected 1:1 ratio in the test-crosses. This indicates that eye pigment is inherited as a simple Mendelian character in these snails. The parental stocks of these 2 populations, separated geographically by a distance of approximately 200 miles, demonstrated mutual cross-fertilization.

In 3 breeding experiments between the albino *Bulinus tropicus* and eye-pigmented *B. natalensis*, the 3 albino parents produced only pigmented F_1 progeny, demonstrating successful cross-fertilization and dominance of eye-pigment. In these successful crosses, there was no embryo mortality. However, the 3 eye-pigmented parents failed to produce progeny. This indicates that the genetic exchange was in only one direction: from pigmented to albino snails.

The observation of the F_2 progeny obtained by brother-sister crosses of F_1 snails showed that 1 set of characters (eye pigment vs. no eye pigment) segregated in the expected 3:1 ratio, and the other 2 sets of characters, i.e., brown shell vs. white shell and medium spire vs. low spire (i.e., L/AL 1.36 vs. L/AL 1.27), the characters segregated in both F_1 and F_2 progeny with various ratios, but also showed brown shell dominant to white shell, and medium spire dominant to low spire. These 2 sets of characters were presumably polygenic in nature. The parental stocks of these 2 populations were separated by a distance of approximately 300 miles.

In 4 breeding experiments between 2 populations of *Bulinus tropicus* widely separated geographically (by a distance of approximately 2,500 miles), one the albino strain from South Africa and the other a pigmented strain from Ethiopia, 2 of the 4 experiments resulted in cross-fertilization of the albino with the pigmented snail to produce eye-pigmented F_1 progeny, although with 25% and 28% embryo mortality. The other 2 albinos produced no eggs, or only non-embryonated eggs. None of the eye-pigmented parents produced eggs when mated with albinos. The direction of genetic exchange was in one direction, i.e., from eye-pigmented to albino snails, as in the crosses between the albino *B. tropicus* and *B. natalensis*.

From the above interpopulational breeding experiments, it is interesting to note that the genetic exchange between the albino *tropicus* and the pigmented *tropicus* and *natalensis* populations decreased as geographical separation increased, i.e., in those crosses that were successful between South African *tropicus* and South African *natalensis* there was no observed embryo mortality, but there was some mortality when South African *tropicus* crossed with Ethiopian *tropicus*.

* * *

THE SUSCEPTIBILITY OF *POMATIOPSIS LAPIDARIA* AND VARIOUS RACES OF *ONCOMELANIA HUPENSIS* TO *PARAGONIMUS WESTERMANI* AND *P. OHIRAI*[1]

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and

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Abstract

Pomatiopsis lapidaria (Say, 1817) and 5 subspecies of *Oncomelania hupensis* Gredler, 1881 were tested for their susceptibility to *Paragonimus westermani* (Kerbert, 1878) and to *P. ohirai* Miyazaki, 1939.

The ova of *Paragonimus westermani* were obtained from the feces of an infected dog and the ova of *P. ohirai* were obtained from experimentally infected rats. The feces were macerated in a Waring blender for 2 minutes and then strained through cheese cloth into a 500 ml beaker. The eggs were allowed to settle for 30 minutes, after which time the supernatant was removed. This process of decanting was repeated until the water became clear. Ova were incubated using the Harada-Mori culture method (Beaver, Malek & Little, 1964, *J. Parasitol.* 50: 128). All *Oncomelania* specimens were lab-reared. *Pomatiopsis lapidaria* specimens were field-collected and maintained in the laboratory for 3 months prior to exposure to *Paragonimus* miracidia. These field-collected snails were checked for possible natural infections by observing for shedding of cercariae and only snails considered uninfected were tested. Lots of 50 snails of the various *O. hupensis* subspecies and 20 *P. lapadaria* were exposed to at least 5 miracidia of *P. ohirai*. Varying numbers (12-42) of snails were exposed to at least 5 *P. westermani* miracidia.

The results agree with previous reports that the races of *Oncomelania hupensis* (*nosophora*, *formosana* and *chiui*) are refractory to infection with *Paragonimus westermani*. We were also able to add *O. h. hupensis*, *O. h. quadrasi* and *Pomatiopsis lapidaria* to the list of non-susceptible snails. We present here the first report of experimental infection of *O. hupensis hupensis* and *P. lapidaria* with *P. ohirai* (with incidence of infection 39.5% and 70.0%, respectively). We report the high infectivity of *O. h. nosophora*

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(100%), *O. h. quadrasi* (96.2%) and *O. h. chiui* (77.1%) with *P. ohirai*, and low infectivity of *O. h. formosana* (19%) with this parasite, which confirm previous studies.

We conclude that the various races of *Oncomelania hupensis* can serve as satisfactory laboratory hosts for maintenance and experimental study of paragonimiasis, especially the intra-molluscan stages. Also, we conclude that the genus *Oncomelania* may serve as a model to study larval antagonism between *Schistosoma japonicum* and non-human *Paragonimus*, which may lead to its use as a biological control measure for oriental schistosomiasis.

* * *

EFFECTS OF SNAIL TISSUE EXTRACTS ON IMMOBILIZATION OF SCHISTOSOME MIRACIDIA

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Abstract

Experiments were undertaken to ascertain whether miracidial immobilization of 5 species of schistosomes, *Schistosoma japonicum*, *S. mansoni*, *S. haematobium*, *Schistosomatium douthitti* and *Gigantobilharzia huronensis*, would occur in tissue extracts of 23 species or strains of snails. Some characteristics of immobilizing substances were also observed. The results obtained to date are summarized as follows: (1) The miracidial immobilization in snail tissue extracts appears principally dependent on physiological characteristics of the species of miracidia. (2) The presence of miracidial immobilizing activity in snail tissue extracts occurred in 29 different combinations between certain miracidia and species or strains of snails. (3) Quantitatively, a wide range of miracidial immobilizing activity was demonstrated, the amount depending on the species of snails used. In general, certain related species of planorbid snails belonging to both the Planorbinae and Bulininae exhibit a high degree of immobilizing activity. A lesser degree of the activity is produced by tissue extracts from several species belonging to the families Lymnaeidae and Physidae, while species of the Amnicolidae had little capability for immobilizing any of the miracidia studied here. (4) In all cases, the combinations of certain miracidia and whole tissue extract of a susceptible snail to its trematode infection show a rather low immobilization. It is suggested that the immobilizing activity present in some snail tissue may act, in part, because of the incompatibility between miracidia and snails. (5) The effects of the extracts from 3 separate tissues (foot, digestive gland and gonad) of various snails on *S. japonicum* miracidia showed similar immobilizing results as the extract prepared from entire soft parts of the snails. Whole tissue extract from various snails showed no activity in immobilizing the miracidia of *S. mansoni* and *S. haematobium*, while the extract from the digestive gland of certain snails immobilized these species of miracidia to a greater degree. (6) At least 2 different kinds of immobilizing substances occur in tissue extract from certain snails. One has "heat labile activity" and is found in whole-body soft tissue but is especially concentrated in foot muscle. The other has "heat stable activity" and is present in the digestive gland of some snails. (7) The heat stable immobilizing activity in the digestive gland of snails is capable of immobilizing miracidia of both compatible and incompatible species. (8) The storage of whole tissue extracts from some *Biomphalaria* and *Bulinus* species for 2 weeks at 5°C does not alter their activities. Foot muscle extract stored at 5°C for 7 days or -20°C for 10 days indicates no significant difference in the activity before and after storage. (9) No loss in immobilizing activity by dialysis with a Visking tube could be detected for foot muscle extract from *Biomphalaria glabrata*.

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A SIMPLE MACROSCOPIC METHOD OF DETERMINING CRYSTALLINE FORMS OF DEPOSITED CALCIUM CARBONATE IN MOLLUSC SHELLS BY INFRARED SPECTRAL ANALYSIS

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Abstract

This study shows the potential value of rapid determination of the macroscopic calcium carbonate structure in molluscs (and other biological specimens) by means of infrared spectroscopy. The method is suitable for both qualitative and quantitative analysis. The work was done on 200 specimens of 22 freshwater mussel species (from the subfamilies Anodontinae and Lampsilinae of the family Unionidae) found in the Muskingum River in Ohio, taking at least 3 samples for analysis from each specimen.

The use of infrared spectroscopy for macroscopic examination of the $CaCO_3$ forms has the advantages of being faster and less tedious than X-ray or electron microscopic methods (more quantitative than the

X-ray film-powder pattern technique), and requires less expensive instrumentation. The use of a powder X-ray diffractometer with a scintillation counter may be more quantitative than infrared analysis, but it is more expensive and time-consuming. While infrared analysis of naturally occuring (and synthetic) samples of $CaCO_3$ is not entirely new, a survey of the literature indicates that biological workers are not making much use of this method.

In the case of the freshwater specimens, all of the calcium carbonate of the shell was shown to be aragonite; the composition of 2 *Strombus gigas* Linnaeus shells was primarily aragonite with a thin surface layer of calcite, and the composition of a fossil oyster shell (*Ostrea* sp.) was found to be entirely calcite. Shell spectra were compared to the spectra of calcium carbonate found in appropriate minerals.

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THE SYSTEMATIC POSITION OF *"LYMNAEA" BULIMOIDES*[1]

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Abstract

The freshwater basommatophoran family Lymnaeidae has been divided previously into a number of species-groups, which generally can be recognized by their distinctive shell features. These groups also have been characterized occasionally by features of radulae and/or soft anatomy. However, the taxonomic groupings based on one set of characters and those based on a different set are not always mutually inclusive.

Lea's (1841) *"Limnaea bulimoides"* is an example of a species which by one set of criteria can be placed in one particular taxon, but by other criteria can be placed in a different taxon. Prior to 1928, this species was assigned to the species-group [genus or subgenus] *Galba* (generally = *Fossaria* in current usage) because of its shell characters: shell relatively small for the family, "turreted," without distinct spiral sculpture, columellar axis smooth, not twisted and without a plait, umbilicus present, sometimes as a "chink," but more often open and deep. These characters especially differentiate *Fossaria* from the group *Stagnicola*, the only lymnaeid generic-level taxon in North America with which *Fossaria* might possibly be confused. A species recognized as closely allied to *F. bulimoides* is Pfeiffer's (1839) *"Limnaea cubensis,"* both species possessing similar shells and bicuspid lateral radular teeth in a species-group otherwise only known to contain species with tricuspid lateral teeth (see Baker, 1911, *The Lymnaeidae of North and Middle America*, Chicago Acad. Sci, Spec. Publ. 3, p 206, 218).

In 1928, Baker (*The fresh water Mollusca of Wisconsin.* Pt. 1 Wisc. geol. & natur. Hist. Surv., p 264) gave special emphasis (over shell characters) to the cusp-condition of the lateral radular teeth by placing those species with fossarid-like shells, but having bicuspid lateral teeth, in the genus *Stagnicola*, which was considered to contain only species possessing bicuspid laterals. This subgroup of *Stagnicola* as defined differed from *Stagnicola* s.s. mainly by its fossarid-like shell; it was formally recognized as the subgenus *Nasonia* (type species, *L. cubensis* Pfr.), a generic-group name found later (Weyrauch, 1964, *Arch. Molluskenk.*, 93: 169) to be preoccupied by an insect and therefore replaced with *Bakerilymnaea*. Walter (1963, in Taylor, Walter & Burch, *Malacologia*, 1: 254) mentioned that the anatomy of *"Stagnicola (Nasonia) bulimoides"* is "similar to, and perhaps indentical with, that of *Fossaria*." However, he presents no data or further pertinent details.

In regard to the assessment of phylogenetic characters in the Lymnaeidae, we have shown (1969, *Malacol. Rev.*, 2: 135; 1971, *Zool. Zh.*, 50: 1158-1168) in the cases of *Radix luteola* and *R. acuminata* of India, and *Lymnaea stagnalis* and *Stagnicola corvus* of Poland, that shell characters are more conservative than some characters of soft anatomy. Therefore, we were interested in determining the merits of shell vs. radular characters in a species of *Bakerilymnaea*, a species with a *Fossaria*-like shell but *Stagnicola*-like radula. The species available to us was *"Stagnicola (Bakerilymnaea)" bulimoides* (Lea) from Rice, Texas. Our method was to compare immunological reactions of foot muscle antigens of *"S." bulimoides* with antibodies produced against similar tissues from species of other species groups (*Austropeplea*, *Bulimnea*, *Fossaria*, *Lymnaea* s.s., *Pseudosuccinea*, *Radix* and *Stagnicola* s.s.). Previously (1968, *Amer. malacol. Union ann. Reps.*, 35: 22-23), we determined that there is an immunological *correspondence* in foot muscle proteins among species within any of the above 7 lymnaeid species-groups (genera in Baker's (1928) usage), and immunological *dissimilarity* between species of 2 different groups. Hence, the technique, while not being helpful in discriminating between closely related species, is especially useful in showing relationships of taxa at the species-group level.

Foot muscle antigens of *"Stagnicola (Bakerilymnaea)" bulimoides* showed complete immunological correspondence with antiserum prepared from foot muscle tissues of *Fossaria obrussa*, while strong

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"non-identity" reactions occurred when "*S. bulimoides*" antigens were tested with all the other lymnaeid antisera, including 2 species of *Stagnicola* s.s. (*S. elodes* and *S. emarginata*). It is therefore concluded that *bulimoides* is a member of the *Fossaria* group, as characters of its shell would imply, rather than belonging to a special subgroup of *Stagnicola*, as characters of its radula led Baker to believe.

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THE SUCCINEID GENUS *QUICKIA*

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Abstract

Succinea is a familiar name to most malacologists, especially those interested in pulmonate gastropods. However, the succineid genus *Quickia*, because of its seeming obscurity, is probably familiar to only a few. Until 1968, *Quickia* was considered a monotypic succineid genus found only in east and west Africa and on some adjacent islands. Prior to my studies (Patterson, 1968, *Malacol. Rev.*, 1:1-13; 1970, *Malacol. Rev.*, 3(1): 25-36; 1971, *Malacol. Rev.*, 4(2): 131-202), Quick (1936, *Ann. Natal Mus.*, 8(1): 19-45) and Odhner (1950, *Proc. malacol. Soc. Lond.*, 28(5): 200-210) published the only anatomical work on the genus. Only now is the probable evolutionary importance of *Quickia* beginning to emerge. *Quickia* is currently known to occur in North and South India, East and West Africa, islands adjacent to East Africa and on many Indian Ocean islands. Such an Afro-Indian distribution is of interest when considered in relation to the current theories of continental drift (see Patterson, 1968).

With regard to anatomical features, *Quickia* is distinguished from other Succineidae by a distinct combination of generic characters. It possesses an unsheathed penis and a tentacle assembly which passes completely to the inside of the terminal genitalia. *Q. calcuttensis* Patterson is contained in its subgenus (*Burchella*) because it possesses a penial apron. The haploid chromosome number of *Quickia* (n=25) and the presence of the well developed penial apron in *Q. calcuttensis* evoke questions concerning the phylogenetic position of *Quickia* and its relationship to other Succineidae. In the Succineinae (the subfamily possessing a penial sheath), the penial nerve innervates mainly the sheath and, according to Cook (1966, *Arch. néerl. Zool.*, 17(1): 1-72), also the penis musculature. In Catinellinae (the subfamily lacking a penial sheath), except for *Q. calcuttensis*, the penial nerve innervates the penis directly. In *Q. calcuttensis*, the penial nerve innervates the penial apron with a branch extending to the penis. Thus, not only does the penial apron appear to be a structure intermediate between the conditions found in the Catinellinae and Succineinae, but also the innervation of the penial nerve seems to bridge the gap between the 2 subfamilies. Morphologically, *Quickia* may be somewhat more closely allied to *Catinella* (Catinellinae). However, *Quickia*'s chromosome number (n=25) is closer to some members of the Succineinae (n=11-24) than to other Catinellinae (n=5-6), the subfamily with which it is currently placed.

More species of Succineidae need to be studied anatomically, cytologically and biochemically before one can, with reasonable confidence, postulate evolutionary trends within the family. Although the Succineidae appear to be a group of great antiquity (see Patterson, 1971), some members appear to exhibit evidence of relatively recent evolutionary change (speciation) which may still be continuing at a significant level.

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ARCHAIC LAND SNAILS OF THE PACIFIC ISLANDS[1]

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Abstract

The land snail families Partulidae, Achatinellidae and Amastridae are considered to be ancient, endemic faunal elements of the Inner Pacific, whose species are now the scattered residual descendants of the earliest land snails that developed from aquatic pulmonate ancestors during the late Paleozoic (Pilsbry, 1900a, *Proc. Acad. natur. Sci. Philad.*, p 561-567; Pilsbry, 1900b, *Ibid.*, p 568-581; Pilsbry, 1916, *Ibid.*, 2: 429-433). While the Amastridae are related to the Holarctic Cionellidae (=Cochlicopidae), the Partulidae and the Achatinellidae have no near relatives on the continents. During the possible 200,000,000 years of their evolution in the middle Pacific, their ancient continental affinities declined and disappeared.

These 3 archaic families (Partulidae, Achatinellidae and Amastridae) are the dominant elements among the land snails of the Polynesian region, although they are associated there with the primitive succineids, the relatively primitive higher pulmonates (endodontids and zonitids) and primitive land prosobranchs (helicinids and assimineids), but not with any modern snails which proliferated in the Eocene (helicids, streptaxids, etc.). They are, therefore, exceptional subjects for the study of evolution and zoogeography.

[1] Supported (in part) by research grant GB-6450 from the National Science Foundation, Washington, D. C.

The Amastridae are restricted to the Hawaiian islands, as are members of the subfamily Achatinellinae of the Achatinellidae. The remaining achatinellids (5 subfamilies) are scattered throughout the Inner Pacific, with nearly every island having at least 1 species. The Partulidae range from Palau to the Marquesas, but have only 3 genera:

Eua - contains only 4 species, 1 in Tonga and 3 in Samoa.

Samoana - has a somewhat wider distribution, and has about 25 species.

Partula - is distributed over a wide area of the Pacific (Palau to the Marquesas, a distance of 5,300 nautical miles), and has over 100 species. The center of speciation for the genus is in the Society Islands, especially Raiatea, Huahine, Moorea and Tahiti.

The 3 genera of the Partulidae are distinguished mainly by their terminal male genitalia, the simplest type being found in *Eua* and the most complex in *Partula*. This fact, coupled with the distribution of the 3 genera (i.e., *Eua* very restricted, *Samoana* wider, *Partula* widest), the fact that *Eua globosa* is found on perhaps the oldest island in the Pacific (Eua I., Tonga group), and the snails' habitats (*Partula* does not occur on any of the islands with *Eua*, but where *Partula* and *Samoana* occur together, *Samoana* is displaced to tips of tall trees or mountain tops), have led to the conclusion that *Eua* is the most ancient (and ancestral genus), and that *Partula* is the most recent and advanced (*Eua* gave rise to *Samoana*, which in turn gave rise to *Partula*).

This is a simple straight-forward scheme, a scheme which further research will either corroborate or revise. Of course, it could be equally well postulated that the direction of evolution was from the more complex to the simpler type of penis, and that the more widespread genus (*Partula*) is the more primitive, those with more restricted distributions (*Eua* and *Samoana*) being more specialized. Recent serological studies by Burch may add some plausibility to the latter alternative. The same immunologically detectable foot muscle proteins of *Partula* are also found in *Samoana* and *Eua*, but both of the latter have several additional proteins, *Eua* more than *Samoana*. The foot muscle proteins of *Samoana* are all found in *Eua*, yet the latter has several additional ones. From this one might postulate that *Partula* gave rise to *Samoana* which then gave rise to *Eua*. Such an assumption is based on the finding that the only taxon of the 3 with all non-unique foot muscle proteins is *Partula*, and when only *Samoana* and *Eua* are considered, it is *Samoana* with the non-unique proteins.

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POSSIBLE FAMILY DISTRIBUTION PATTERNS IN PULMONATE GASTROPODS[†]

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Abstract

Alfred Russel Wallace (1876, *The geographical distribution of animals*, Vols. 1 & 2, Harper & Bros., New York, 503 + 607 p) contrasted 2 different aspects of zoogeography: "zoological geography", which is the study and cataloging of the fauna in a particular geographic region; and "geographical zoology", the study of faunal distribution and their geographic relationships by taxonomic group. The present study belongs to the latter type of zoogeography. Specifically its aim is to delimit the number and kinds of distribution patterns at the family level. The results presented here are of tentative nature, pending more definitive study.

All 3 orders of the Pulmonata are included. The classification followed is basically that of Taylor & Sohl (1962, *Malacologia*, 1: 7-32). Distribution information is taken from Zilch (1959-60, In: Schindewolf, *Handb. Paläozool.*, Lief. 1-4, 6: 834 p, Borntraeger, Berlin) and the base map used is *Stieler's Hand-Atlas* (1926-28, 10th ed., J. Perthes, Gotha, 316 p).

The Basommatophora show 2 major patterns, families with world-wide distribution and the endemics. The Systellommatophora show only 1 pattern, the pantropical. The Stylommatophora, which is the biggest of the 3 orders, shows 12 major patterns and several subpatterns. These 12 patterns can be taken to represent the entire pulmonate group, since the 2 other orders can be accommodated in one or another of the 12 patterns. These 12 patterns are listed in Table 1.

Table 2, shows a list of families assigned to each of the patterns. A single asterisk (*) indicates endemicity, while double asterisks (**) indicate the family is highly endemic, or confined to a small part of the pattern to which it is assigned. Figures in parenthesis show the number of genera and subgenera of the family as taken from Zilch (1959-1960); this is to indicate the relative size of the family. Note that the figure given is a total figure which includes both fossil and living groups and also groups that are questionable. Family names in parenthesis indicate that the family might possibly be included in that particular pattern, but actually are placed in another pattern. Patterns of distribution are based only on Recent pulmonate gastropods.

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TABLE 1. List of zoogeographic patterns in the Pulmonata, arranged by geographic sequence

I World-wide
  a) Nearly world-wide
II Pantropical
III Holarctic
  a) Nearly Holarctic
IV Palaearctic
  a) Extended to Africa and the Orient (Old World)
V Western Palaearctic
  a) Extended to the Tropics
  b) Extended to North America
VI Africa
VII Africa-Oriental-Manchurian Palaearctic
  a) Extended to southwestern Siberia
VIII Oriental-Pacific
IX Pacific-Australian
  a) Extended to East Asia and Americas
X East Asia-Americas
  a) Extended to Pacific-Australian
XI Americas
  a) North, Middle and South Americas
  b) North America
  c) Middle America
    c') Extended to Mediterranean
    c'') Extended to North America
  d) South America
    d') Extended to Pacific-Australian
    d'') Extended to Africa
XII Southern distribution

TABLE 2. List of families of Pulmonata tentatively placed under each distribution pattern

A. SYSTELLOMMATOPHORA

I Pantropical
  1. Veronicellidae (16)[1]

B. BASOMMATOPHORA

I World-wide
  1. Planorbidae (84)
  2 Ellobiidae (55)
  3 Lymnaeidae (34)
  4 Siphonariidae (19)
  5 Ancylidae (15)
  6 Physidae (6)
  7 Trimusculidae (1)

II Endemic and Semi-endemic
  8 Acroloxidae (3). . . . Europe and Baikal Lake (Siberia) also North America
  *9 Lancidae (4). . . . . North America
  10 Amphibolidae (2). . . East Asia, Australia, Pacific
  **11 Otinidae (2). . . . . Coast of southwestern British Isles and northern France
  **12 Chilinidae (1). . . . . Southern South America
  **13 Latiidae (1). . . . . New Zealand

C. STYLOMMATOPHORA

I World-wide
  1 Endodontidae (106)
  2 Vertiginidae (39)
  3 Chondrinidae (34)
  4 Pupillidae (27)
  5 Succineidae (26)
  6 Valloniidae (19)
  a) Nearly World-wide
  7 Clausiliidae (227)
  _ (Camaenidae) (102)
  _ (Euconulidae) (94)
  _ (Subulinidae) (80)

II Pantropical
  8 Streptaxidae (87)
  9 Subulinidae (80)
  _ (Ferrussaciidae) (20)

III Holarctic
  10 Zonitidae (93)
  11 Vitrinidae (14)
  12 Cionellidae (4)
  a) Nearly Holarctic
  13 Arionidae (24)
  _ (Limacidae) (26)

[1]Classification differs from Taylor & Sohl (1962).

TABLE 2 (cont.)

IV Palaearctic
14 Pyramidulidae (1)

a) Extended to Africa and the Orient (Old World)
15 Enidae (80)
_ (Bradybaenidae) (80)
_ (Ariophantidae) (73)

V Western Palaearctic
16 Helicidae (192)
**17 Trigonochlamydidae (7)[18]
*18 Orculidae (5)[3]
*19 Parmacellidae (5)[4]
*20 Milacidae (4)[5]
*21 Testacellidae (3)[6]
*22 Pleurodiscidae (1)[7]

a) Extended to the Tropics
23 Ferrussaciidae (20)

b) Extended to North America
24 Limacidae (26)

VI Africa
*25 Urocyclidae (44)[8]
*26 Achatinidae (23)[9]
**27 Dorcasiidae (3)[19]
**28 Aillyidae (1)[20]
**29 Chlamydephoridae (1)[21]
**30 ?Thyrophorellidae (1)[22]

VII Africa-Oriental-Manchurian Palaearctic
31 Corillidae (8)

a) Extended to Southwestern Siberia
32 Bradybaenidae (80)
33 Ariophantidae (73)

VIII Oriental-Pacific
34 Helicarionidae (69)
35 Trochomorphidae (24)

IX Pacific-Australian
36 Achatinellidae (23)
**37 Amastridae (19)[23]
*38 Partulidae (12)[10]
*39 Athoracophoridae (1)[11]
**40 Otoconchidae (1)[24]
_ (Rhytididae) (19)

a) Extended to East Asia and Americas
41 Euconulidae (94)

X East Asia-Americas
42 Philomycidae (1)

a) Extended to Pacific-Australian
43 Camaenidae (94)
_ (Euconulidae) (94)

XI Americas
a) North, Middle and South Americas
44 Helminthoglyptidae (51)

b) North America
45 Polygyridae (34)
46 Haplotrematidae (8)
*47 ?Ammonitellidae (5)[12]
*48 Oreohelicidae (2)[13]

c) Middle America
*49 Urocoptidae (79)[14]
*50 Sagdidae (21)[15]
**51 Oleacinidae (12)[25]
**52 Cerionidae (5)[2,26]

c') Extended to Mediterranean
53 Spiraxidae (44)
c'') Extended to North America
54 ?Thysanophoridae (10)

d) South America
55 Orthalicidae (17)
*56 Odontostomidae (16)[16]
57 ?Systrophiidae (14)
*58 Strophocheilidae (7)[17]

d') Extended to Pacific-Australian
59 Bulimulidae (94)

d'') Extended to Africa
60 Amphibulimidae (8)

XII Southern Distribution
61 Rhytididae (19)
62 Acavidae (12)
63 Megaspiridae (5)
_ (Bulimulidae) (94)
_ (Odontostomidae) (16)
_ (Amphibulimidae) (8)
_ (Strophocheilidae) (7)
_ (Dorcasiidae) (3)
_ (Athoracophoridae) (1)
_ (Chlamydephoridae) (1)
_ (Otoconchidae) (1)

[2]Nomenclature differs from Taylor & Sohl (1962).
[3]Orculidae ... southern Europe
[4]Parmacellidae ... western Palaearctic
[5]Milacidae ... western Palaearctic
[6]Testacellidae ... southwestern Europe and North Africa
[7]Pleurodiscidae ... southern Italy, some Mediterranean islands, southern and eastern Mediterranean region
[8]Urocyclidae ... Africa
[9]Achatinidae ... Africa
[10]Partulidae ... High islands of southern and western Pacific
[11]Athoracophoridae ... South Pacific islands
[12]?Ammonitellidae .. western North America
[13]Oreohelicidae ... western North America
[14]Urocoptidae ..... Middle America, extend slightly to southern North America and northern South America
[15]Sagdidae ... Middle America
[16]Odontostomidae ... South America
[17]Strophoceilidae ... South America
[18]Trigonochlamydidae .... Caucasus-Persian region
[19]Dorcasiidae ... South and southwest Africa
[20]Aillyidae ... Cameroon (West Africa)
[21]Chlamydephoridae ... South Africa
[22]?Thyrophorellidae ... Sao Tome island (Gulf of Guinea, West Africa)
[23]Amastridae ... Hawaiian islands
[24]Otoconchidae ... New Zealand
[25]Oleacinidae ... West Indies and south Florida
[26]Cerionidae ... West Indies

* * *

DEVELOPMENTAL REGULATION OF THE TROCHOPHORE OF *NASSARIUS*

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Abstract

Nassarius (*Ilyanassa*) *obsoletus* passes through the trochophore stage within the egg capsule. The typical structures of the trochophore are reduced so that the apical tuft which forms on the apical plate cells $1a^{111}$-$1d^{111}$, $1a^{1121}$, $1b^{1121}$ and $1b^{1211}$ is composed of short motile cilia rather than long sensory ones. Lateral tufts of short cilia on $1a^{21}$ and $1b^{21}$ are the only vestiges of the prototroch. Removal of the 1st or 2nd polar lobe or the D quadrant macromere results in development of cilia over most of the pretrochal region, so that unciliated cells of the control embryo develop cilia in the operated embryos. It is proposed that the polar lobe normally inhibits ciliation in those cells whose prospective fate is to form unciliated cephalic plate cells. Ciliation can occur in the absence of DNA-dependent RNA synthesis, judged from actinomycin treatment, and in the absence of RNA-dependent protein synthesis, judged from puromycin treatment, suggesting that regulation occurs at a post-translational level and most likely at that time of the assembly of tubulin into cilia. A relationship between the number of cleavages and the degree of ciliation was noted.

* * *

OF SHELLS AND TIME

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Abstract

At present, the geologic record shows that the classes of the Mollusca appeared in the following order - Early Cambrian: Monoplacophora and Gastropoda; Middle Cambrian: Bivalvia; Late Cambrian: Polyplacophora and Cephalopoda; Ordovician: Scaphopoda. Radiometric ages for Cambrian and Ordovician rocks show the origin of the Gastropoda to be some 50 to 100 million years; that of the Monoplacophora and Bivalvia about 50 million years apart. This provides ample time for the evolution of classes one from another. These data should be kept in mind by evolutionists and text-book writers. The axiom that a Middle Cambrian class can not be descended from an Ordovician one is so obvious that it is often forgotten. If hypothetical phylogenies are to be constructed, they must rest on known data, scanty as they may be.

In a more restricted field, carbon-14 dates give us a number of reference points on which to reconstruct the development and migrations of the Mollusca in Pleistocene time. For example, we now have dates of more than 35,000 years before present for Ross County, Ohio with an identified freshwater molluscan fauna (*Pleistocene Mollusca of Ohio*, pt. 1, p 40-41); the Sidney Cut faunule (*op. cit.*, p 43-44) is more than 37,000 years old and many more deposits containing successive molluscan faunules have now been dated in the Midwest. This should influence our thinking on 2 points. First, the routes of migration of non-marine Mollusca as they repopulated territory freed from continental glaciers can be traced with some accuracy. Secondly, these dates place limits on the time during which new species, subspecies, or forms could have evolved during the Pleistocene. They give us pause when we are tempted to name new taxa on what may be nothing more than isolated populations with minor shell peculiarities that lasted no more than an instant in geologic time.

Biologists attending the Mollusk Seminar, Ann Arbor, Michigan, U.S.A., 6 August 1971. Left to right: Esther M. Goudsmit, Gene K. Lindsay, Edward L. Compere, Jr., Henry van der Schalie, Carol B. Stein, James E. Pietrzak, David H. Stansbery, Aurèle LaRocque, Donald J. Klemm, Gary L. Pace, Shi-Kuei Wu, Philip T. Clampitt, Philip T. LoVerde, Amy L. Shrader, Carolyn Jenkinson, John Jenkinson, James N. Cather, C. M. Patterson, Isaac S. Dumbo, George A. Te, Yung-San Liang, J. B. Burch.

MISCELLANEA

THE FOURTH MEETING ON MOLLUSC STUDIES, U.S.S.R. — On 10-12 March 1971 the Fourth Meeting on Mollusc Studies was held in Leningrad at the Zoological Institute of the U.S.S.R. Academy of Sciences. It was convened by the Malacological Committee of the Scientific Council on the problem of "Biological bases of management, conservation and reconstruction of fauna". The themes of this Meeting, as well as those of the 3 previous ones held in 1961, 1965 and 1968, showed various aspects of mollusc studies underway in the U.S.S.R. At the most recent Meeting much attention was paid to summarizing the results of researches and discussing ways and methods for further studies. One hundred eighty-four scientists participated in the Meeting, representing 52 research units from 29 cities in the U.S.S.R.

A booklet (*Molluscs: Trends, methods and some results of their investigation*, p 1-158, Leningrad, 1971, Ed., I. M. Likharev) containing abstracts of the papers of the Fourth Meeting was issued after the Meeting. The contents of this booklet are given on the following pages of *Malacological Review* (p 24-27). It contains abstracts of 88 papers, more than 50 of which were read before the Meeting. The rest were discussed during the debate.

Five papers dealt with the main problems and perspectives of mollusc studies. Among them were the papers, "The main problems of morphological, systematic and phylogenetic studies of mollusks in the U.S.S.R. (prepared by a group of malacologists of the Zoological Institute of the U.S.S.R. Academy of Sciences and the Leningrad State University), and "Results and perspectives of studies of fossil freshwater mollusks" by G. G. Martinson. In several papers possibilities and perspectives of applying new methods in taxonomic studies were shown, such as electron microscope investigations (I. S. Barskov), electrophoresis of myogens (B. M. Longvinenko and O. P. Kodolova), experimental interbreeding (N. D. Kruglov), etc.

Some basic problems of systematics and phylogeny were discussed, e.g., development of bivalves during geological time (L. A. Nevesskaya), Soleolifera being a particular subclass of gastropods (Yu. S. Minichev), etc.

A considerable number of papers dealt with ecology, physiology, life cycles and reproductive peculiarities of molluscs. Much attention was also paid to abundant commercial shellfishes, to the malacofauna of seas of eastern U.S.S.R., to the fauna and zoogeography of freshwater and terrestrial molluscs in various regions of the U.S.S.R. which previously were poorly studied, and to the development of caenozoic malacofaunas. A series of papers was dedicated to the role of molluscs as helmintic disease vectors, to molluscs and trematode larvae interrelations, and to the control of harmful molluscs.

The most significant conclusions were summarized in the resolution accepted. At the end of the Meeting a new staff of the Malacological Committee was elected, I. M. Likharev being the chairman and Ya. I. Starobogatov the scientific secretary.

O. A. SCARLATO

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АКАДЕМИЯ НАУК СССР
ЗООЛОГИЧЕСКИЙ ИНСТИТУТ
НАУЧНЫЙ СОВЕТ ПО ПРОБЛЕМЕ «БИОЛОГИЧЕСКИЕ ОСНОВЫ ОСВОЕНИЯ, РЕКОНСТРУКЦИИ И ОХРАНЫ ЖИВОТНОГО МИРА»
ACADEMY OF SCIENCES USSR
ZOOLOGICAL INSTITUTE

ЧЕТВЕРТОЕ СОВЕЩАНИЕ ПО ИЗУЧЕНИЮ МОЛЛЮСКОВ
FOURTH MEETING OF THE INVESTIGATION OF MOLLUSCS

МОЛЛЮСКИ
ПУТИ, МЕТОДЫ И ИТОГИ ИХ ИЗУЧЕНИЯ
MOLLUSCS
TRENDS, METHODS AND SOME RESULTS OF THEIR INVESTIGATION

АВТОРЕФЕРАТЫ ДОКЛАДОВ

СБОРНИК ЧЕТВЕРТЫЙ

THESES OF COMMUNICATIONS

Под редакцией И. М. ЛИХАРЕВА
Edited by I. M. Likharev

ИЗДАТЕЛЬСТВО «НАУКА»
ЛЕНИНГРАДСКОЕ ОТДЕЛЕНИЕ
Ленинград
1971

ПРЕДИСЛОВИЕ

Настоящий сборник составлен из авторефератов докладов, которые представлены на Четвертое совещание по изучению моллюсков, созываемое Малакологическим комитетом Научного совета «Биологические основы освоения, реконструкции и охраны животного мира». Совещание будет проходить в марте 1971 г. в Зоологическом институте Академии наук СССР (Ленинград).

Тематика сборника, как и аналогичных сборников, выпущенных к предшествующим совещаниям, достаточно разнообразна и обширна, что указывает на широкий диапазон научных интересов и направлений исследований малакологов СССР. Наряду с докладами, подводящими итоги и указывающими дальнейшие пути развития советской малакологии, существенное место занимают работы по систематике, фаунистике, истории фауны, по экологии и экологической физиологии моллюсков.

Все вопросы и замечания по четвертому сборнику просьба направлять по адресу: Ленинград, В-164, Университетская набережная, 1, Зоологический институт Академии наук СССР, Малакологическому комитету.

FOREWORD

This volume comprises summaries of reports, presented to the 4 Meeting on molluscan research, being arranged by Malacological committee of Scientific council «Biological bases for using, reconstruction and protection of animals». Meeting will be held on March 1971 in Zoological Institute of the Academy of Sciences of the USSR (Leningrad).

The themes of the reports of this volume, like those of analogous volumes, issued for the preceding meetings are rather diverse and broad, which points at the wide range of scientific interests and trends in research made by malacologists of the USSR.

Works on the taxonomy, faunas, faunas history, ecology and ecological physiology of molluscs as well as reports summing up the efforts of Soviet malacology and indicating its further directions of development, occupy an important place in this volume.

Please send all the questions and criticism for this volume to the following address: Malacological committee, Zoological Institute of the Academy of Sciences of the USSR, Universitetskaja naberezhnaja, 1, Leningrad, B-164, USSR.

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TITLES OF *LEAFLETS IN MALACOLOGY*

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LEAFLETS IN MALACOLOGY

Editor and Publisher S. STILLMAN BERRY Redlands, California

INCEPTION

The intent of this modest sheet is to open an avenue for undelayed publication and dissemination among interested students of notices of new mollusks of special interest under study in the laboratory of the editor, wherever definition on a preliminary basis appears desirable for purposes of extraneous discussion; to set forth occasional hypotheses or tentative arrangements for corrective criticism and testing by other students; and to record short studies for which no more appropriate medium may presently be available.

MAY 3, 1947 VOL. 1, NO. 2

A SURPRISING MOLLUSCAN DISCOVERY IN DEATH VALLEY

BY S. STILLMAN BERRY

OCTOBER 1, 1947 VOL. 1, NO. 3

ON THE GENERIC RELATIONSHIPS OF CERTAIN LOWER CALIFORNIAN HELICOID SNAILS

BY S. STILLMAN BERRY

FEBRUARY 20, 1948 VOL. 1, NO. 4

TWO MISUNDERSTOOD WEST AMERICAN CHITONS

BY S. STILLMAN BERRY

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OCTOPUS BITES IN HUMAN BEINGS

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Division of Medical Zoology
School of Tropical and Preventive Medicine
College of Medical Evangelists
Loma Linda, California

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A NEW OPISTHOTEUTHIS FROM THE EASTERN PACIFIC

BY S. STILLMAN BERRY

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THREE NEW PYRGULOPSIS FROM THE COLORADO DESERT, CALIFORNIA

BY DWIGHT W. TAYLOR
Museum of Zoology, University of Michigan

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A PARTIAL REVIEW OF SOME WEST AMERICAN SPECIES OF CREPIDULA

BY S. STILLMAN BERRY

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Pomona College, Claremont, California

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OCTOPUS BITES — A SECOND REPORT.

BY S. STILLMAN BERRY, Redlands, California
and BRUCE W. HALSTEAD, M.D.,
Division of Medical Zoology, School of Tropical and Preventive Medicine
College of Medical Evangelists, Loma Linda, California.

JULY 1, 1954 VOL. 1, NO. 12

WEST AMERICAN MOLLUSCAN MISCELLANY.—I.

BY S. STILLMAN BERRY

JULY 9, 1956 VOL. 1, NO. 13

DIAGNOSES OF NEW EASTERN PACIFIC CHITONS

BY S. STILLMAN BERRY

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NOTICES OF NEW EASTERN PACIFIC MOLLUSCA.—I.

BY S. STILLMAN BERRY

March 28, 1958 Vol. 1, No. 15

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Editor and Publisher S. Stillman Berry Redlands, California

NOTICES OF NEW EASTERN PACIFIC MOLLUSCA.—II.

BY S. STILLMAN BERRY

May 31, 1958 Vol. 1, No. 16

WEST AMERICAN MOLLUSCAN MISCELLANY.—II.

BY S. STILLMAN BERRY

July 29, 1959 Vol. 1, No. 17

THE GENERITYPE OF NENIA H. AND A. ADAMS.

BY JOSHUA L. BAILY JR., SC.D

Research Associate in Malacology, San Diego Society of Natural History.

July 29, 1959 Vol. 1, No. 18

NOTICES OF NEW EASTERN PACIFIC MOLLUSCA—III.

BY S. Stillman Berry

Dec. 31, 1960 Vol. 1, No. 19

NOTICES OF NEW EASTERN PACIFIC MOLLUSCA—IV.

BY S. Stillman Berry

Nov. 13, 1962 Vol. 1, No. 20

LEAFLETS IN MALACOLOGY

Editor and Publisher S. Stillman Berry Redlands, California

Editorial Note: It is a source of gratification to be able to offer in these Leaflets the last molluscan paper from the eminent pen of the late Dr. Ralph Arnold. Originally intended for publication in an earlier issue, the unfortunate intervention of his death conspired with an illness of the editor to effect postponement until the present. The paper was first written for the 1959 Redlands meeting of the American Malacological Union, Pacific Division, before which, in view of the author's frail health, it was duly presented in his stead by his friend and associate, George H. Ide. The paper is of enduring interest for the autobiographical notes it contains and its nostalgic account of early collecting days in southern California before the crowds poured in. It is here presented as written, without alteration other than a minor smoothing of the discourse in a few places. Certain formal biographical data given in Mr. Ide's abstract in A.M.U. Bulletin 26 for 1959, p. 38-39, are not reprinted.—S.S.B.

EIGHTY YEARS EXPERIENCE AS A CONCHOLOGIST

BY Ralph Arnold

FEBRUARY 5, 1963 VOL. 1, No. 21

LEAFLETS IN MALACOLOGY

Editor and Publisher S. STILLMAN BERRY Redlands, California

THE ENIGMA OF A HITCH-HIKING SNAIL

BY JOHN E. FITCH

California State Fisheries Laboratory, Terminal Island

MARCH 29, 1963 VOL. 1, No. 22

DIAGNOSES OF NEW EASTERN PACIFIC CHITONS—II

BY S. STILLMAN BERRY

This paper is in continuation of that appearing in 1956 as No. 13 of these Leaflets.

SEPT. 30, 1963 VOL. 1, No. 23

NOTICES OF NEW EASTERN PACIFIC MOLLUSCA.—V

BY S. STILLMAN BERRY

The present paper continues the series of which Leaflet No. 19 was the last to appear, and serves the same purpose. Available type-material is designated for distribution according to the plan previously outlined. These accounts are merely preliminary. More detailed descriptions with appropriate illustrations are in current preparation for subsequent publication elsewhere. I continue deeply and appreciatively in debt to the various collectors cited for the materials utilized.

JULY 29, 1964 VOL. 1, No. 24

NOTICES OF NEW EASTERN PACIFIC MOLLUSCA—VI

BY S. STILLMAN BERRY

The present paper continues the series of which Leaflet No. 23 was the last to appear, and serves the same purpose. Available type-material is designated for distribution according to the plan already outlined. These accounts are purely preliminary. More detailed descriptions with appropriate illustrations are in current preparation for subsequent publication elsewhere. And I am again happy to acknowledge my continuing debt to the various collectors cited for their kind generosity in supplying key materials for my studies.

SEPTEMBER 26, 1968 VOL. 1, No. 25

NOTICES OF NEW EASTERN PACIFIC MOLLUSCA—VII

BY S. STILLMAN BERRY

This paper is in continuation of a series the last of which was contained in Leaflet No. 24. It serves the same purpose and is subject to the same introductory explanations as the earlier members of the series. It should be added that since the issuance of No. VI my resources for the study of the mollusks of this region have been greatly extended by the acquisition of various important items from the older and relatively inaccessible relevant literature and the accession of much important new study material, particularly the remarkable Margaret S. Cunningham West Mexican Collection, which at last places me in a position to complete several major studies long slowly building up on my desk.

DECEMBER 17, 1969 VOL. 1, NO. 26

LEAFLETS IN MALACOLOGY

Editor and Publisher S. STILLMAN BERRY Redlands, California

NOTICES OF NEW EASTERN PACIFIC MOLLUSCA—VIII

BY S. STILLMAN BERRY

The present contribution to this series was intended to follow its predecessor (Leaflet No. 25) almost immediately, but a long and serious illness on the part of the writer intervened, with continuance possible only now. The delay has been unfortunate, but it is hoped that none of the items dealt with have lost in interest thereby. Here established as new specific taxons are the second *Rimula* from the area under study, a noble *Turcica*, two *Crucibulum*, one of them possibly the giant of the genus, an *Acanthotrophon*, a fine *Mitra*, a colorful *Oliva*, a striking turrid, and a *Siphonaria*. All of these but the last inhabit the Panamic Province, and all but the *Acanthotrophon* are West Mexican. More detailed descriptions and illustrations have been prepared for forthcoming papers. As many of the figures as possible are meanwhile being made available to Dr. A. Myra Keen for use in the revision of her classic book on the Panamic fauna now in progress.

Malacological Review, 1972, 5: 33-34

TITLES IN *GASTROPODIA*[1]

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Vol. 1, No. 1, October 15, 1952, 8 pages (pages not specifically numbered)

Glenn R. Webb. Pulmonata, Xanthonycidae: Comparative sexological studies of the North American land-snail, *Monadenia fidelis* (Gray) — a seeming ally of Mexican helicoids. p 1-3.
Glenn R. Webb. Beneficial — *Cepaea nemoralis* and cardinals. p 7-8.
Glenn R. Webb. Snail-conservation needs. p 8.
Glenn R. Webb. Pulmonata, Helminthoglyptidae: Sexological data on the land-snails, *Cepolis maynardi* & *Helminthoglypta traski fieldi* and their evolutionary significance. p 4-5.
Glenn R. Webb. Pulmonata, Philomycidae: Anatomical data on the slugs *Pallifera dorsalis*, *P. fosteri* and a new subspecies. p 6-7.
Glenn R. Webb. Pulmonata, Polygyridae: A sexological revision of some triodopsin land-snails, *Xolotrema*, *Neohelix*, & *Wilcoxorbis*. p 7-8.

Vol. 1, No. 2, June 4, 1954, p 9-20

Morris K. Jacobson. *Discus rotundatus* (Müller) in New Jersey and New York. p 9-10.
Ralph H. Humes. A new color form of *Liguus*. p 10.
Glenn R. Webb. Pulmonata, Succineidae: *Succinea* (*Desmosuccinea*) *pseudavara*, new section and species. p 10, 18-19.
Glenn R. Webb. The life-history and sexual anatomy data on *Ashmunella* with a revision of the triodopsin snails. p 13-18.
Glenn R. Webb. Pulmonata, Polygyridae, Polygyrinae: The sexology and taxonomy of seven species of land-snails of the genus *Mesodon*. p 19-20.
Glenn R. Webb. *Quickella* (*Mediappendix*) *oklahomarum loculosa* n. subsp. p 20.
Glenn R. Webb. Zonitoidae: *Ventridens ligerus* (Say) mating. p 20.

Vol. 1, No. 3, February 14, 1959, p 21-28

Glenn R. Webb. Two new north-western slugs, *Udosarx lyrata*, and *Gliabates oregonia*. p 22-23.
Ernest J. Roscoe. An additional record of *Lymnaea auricularia* from Utah. p 23.
Glenn R. Webb. Pulmonata, Polygyridae: Notes on the sexology of *Triodopsis*, a new sub-genus, *Haroldorbis*, and a new section, *Shelfordorbis*. p 23-25.
Glenn R. Webb. Polygyridae: A semi-albino *Mesodon pennsylvanicus* (Green). p 26.
Glenn R. Webb. *Quickella wandae* Webb in eastern Iowa. p 26.
Glenn R. Webb. *Succinea pseudavara* Webb in Texas. p 26.

Vol. 1, Nos. 4-5, November 27, 1961, p 29-52

Glenn R. Webb. Studies on the sexology and development of the genitalia of *Glyptostoma gabrielense* Pilsbry. p 29-30.
Glenn R. Webb. The phylogeny of American land snails with emphasis on the Polygyridae, Arionidae, and Ammonitellidae. p 31-44, 45, 47-49, 51.
Glenn R. Webb. The sexology of three species of limacid slugs. p 44, 46, 50, 52.

Vol. 1, No. 6, September 4, 1965, p 53-60

Glenn R. Webb. The sexology of three species of limacid slugs (cont.). p 53-54.
Glenn R. Webb. Outdoor observations on land-snail feeding habits. p 55-58.
Glenn R. Webb. On the sexology of *Trilobopsis loricata sonomaensis* (Hemphill). p 58-60.
Gary Coller. *Arion circumscriptus* and *Arion subfuscus* in Reading, Berks County, Pennsylvania. p 60.

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[1]Editor, Glenn R. Webb, Kutztown State College, Kutztown, Pennsylvania 19530, U. S. A.

Vol. 1, No. 7, March 1, 1968, p 61-72

Glenn R. Webb. Observations on the sexology of *Philomycus carolinianus* (Bosc). p 62.
Glenn R. Webb. Notes on the sexology of the polygyrid land-snail, *Mesodon sargentianus* (Johnson & Pilsbry). p 62-65.
Glenn R. Webb. Sexological notes on *Mesodon* (*Ragsdaleorbis*) *christyi* (Bland). p 66.
Glenn R. Webb. Observations on the sexology of the endodontid land-snail, *Anguispira alternata* (Say). p 66-67.
Glenn R. Webb. Sexological notes on *Ventridens elliotti*, *V. acerra*, *V. demissus brittsi*, and *V. ligera*. p 67-70.
Glenn R. Webb. The Ashmunellinae: Sexological notes on *Allogona*. p 70-72.

Vol. 1, No. 8, December 26, 1970, p 73-84

Glenn R. Webb. Sexological notes on *Cryptomastix mullani* (Bland and Cooper). p 74-75.
Glenn R. Webb. Observations on the sexology of *Vespericola columbiana* (Lea) from Olympic Peninsula, Washington. p 75-77.
Glenn R. Webb. Fragmentary observations on sexology of *Cryptomastix hendersoni* Pilsbry and *C. magnidentata* Pilsbry and a new subgenus (Pulmonata, Polygyridae, Ashmunellinae). p 77-78.
Glenn R. Webb. Anatomical topotypes of *Trilobopsis penitens* (Hanna & Rixford) from Mormon Island, California. p 78-79.
Glenn R. Webb. Pulmonata, Camaenidae: Comparative sexology and genital development of *Caracolus caracolla* (L.), *C. marginella* (Gmelin), and *Polydontes lima* (Ferussac). p 79-84.

MEETING NOTICES

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THE MALACOLOGICAL SOCIETY OF JAPAN, 45th ANNIVERSARY. — The Malacological Society of Japan intends to celebrate the 45th Anniversary in May 1973 in Tokyo, and the officers of the Society inhabiting Tokyo are polishing up a plan in detail as to the date, place and event. In the past the events have included memorial addresses, statement of research results, exhibition of shell specimens and literature, and similar events will probably be scheduled for the current meetings.

WESTERN SOCIETY OF MALACOLOGISTS. — The Fifth Annual Meeting of the Western Society of Malacologists will be hosted by the Yucaipa Shell Club at the University of Redlands, Redlands, California during 18-21 June 1972. There is no special theme for the meeting and papers on all aspects of malacology will be accepted. However, papers are desired which can add qualitative and quantitative information falling within the areas of ecology, conservation, pelecypoda, gastropod spawning and spawning products and with Opistobranchia. The program is being coordinated by Mrs. Beatrice L. Burch, WSM President, 236 Kuuhoa Place, Kailua, Hawaii 96734, U.S.A., in cooperation with Dr. Donald Shaskey, 734 W. Highland Avenue, Redlands, California 92373.

Sessions. In arranging the program, the President and Symposia Chairmen will schedule related papers or similar topics in the same session. Chairmen are: Pelecypoda - Dr. Vida Kenk; Opistobranchia - M. Wesley Farmer; Gastropod Spawning and Spawning Products - Dr. George Radwin; Ecology - Dr. James Nybakken; and Conservation - Hans Bertsch, O.F.M. Other chairmen are: Student Papers - Mr. James Carlton; Displays - Mr. Ted Phillips; and Hospitality - Mr. and Mrs. E. E. Wahrenbrock. The Local Coordinator between the Club and University is Dr. Don Shasky. The Auctioneer is Mr. Glenn Burghardt.

There will be a workshop session on various aspects of malacology. These will be intimate working groups coordinated by workshop chairmen especially in the following topics: Pelecypod identification - Dr. Eugene Coan and Dr. Myra Keen; Minute Gastropods - Mr. Bertram Draper; and Shell Art - Mrs. E. E. Wahrenbrock.

AMERICAN MALACOLOGICAL UNION. — The 38th annual meeting of the American Malacological Union will be held at Galveston, Texas, on July 9-14, with Dr. Arthur S. Merrill presiding. Details of arrangements will be sent to members by way of Newsletters during the coming year. Those interested in the American Malacological Union should contact the Recording Secretary, Mrs. Marian S. Hubbard, 3957 Marlow Court, Seaford, New York 11783, U. S. A.

MOLLUSK SEMINAR AT THE UNIVERSITY OF MICHIGAN, August 1972. — A seminar on Multi-disciplinary Contributions to the Study of Systematics and Evolution of Mollusks will be held at the Museum of Zoology, the University of Michigan, Ann Arbor, Michigan 48104, U.S.A. on 25 and 26, August 1972. The object of the seminar will be to bring together researchers working toward common ends but using a variety of methods in studying mollusks. Areas covered will be morphology, embryology and development, cytology, genetics, physiology, biochemistry and serology, numerical data processing, and ecology and zoogeography. The seminar will be informal, and will consist of a series of brief presentations by participants followed by brief discussions. More extensive discussions may be arranged in subjects of special interest.

Those wishing to attend or to participate in the seminar should contact the organizer of the symposium, J. B. Burch, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104, U. S. A.

THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND, PROGRAMME OF MEETINGS FOR 1972. — During the current year the Society is sponsoring the following topics for exhibition and discussion:

Tertiary Fossils. "Corbulidae," by Dr. A. J. Rundle, 15 January 1972.

Annual General Meeting. "Origin and distribution of non-marine Mollusca in South America," Presidential Address by T. Pain, 26 February 1972.

Conservation. "Conservation and the countryman," by Rt. Hon. the Earl of Cranbrook, 18 March 1972.

Caribbean Mollusca. "Through the Everglades in a pair of carpet slippers," by S. P. Dance, 15 April 1972.

Shells with Spines and Bristles. "Hairy snails," by Dr. June Chatfield, 21 October 1972.

The Development of Faunas in the North Sea Basin. "Faunas in the southern part of the North Sea with particular reference to the East Anglian Crags," by P. Cambridge, 18 November 1972.

Gourmetlacology. "The art of cooking and eating shellfish, by J. Llewellyn Jones, 16 December 1972.

Meetings will be held in the Rooms of the Linnean Society, Burlington House, Piccadilly.

Notice of summer *Field Meetings* will appear in the Society's Newsletter. For additional information about the Conchological Society of Great Britain and Ireland or its affairs write Mrs. E. B. Rands, Hon. Secretary, 51 Wychwood Ave., Luton Beds., LU2 7HT, U.K.

THIRD ANNUAL SYMPOSIUM OF THE ISRAEL MALACOLOGICAL SOCIETY. — The Third Annual Symposium, to be held in April, 1973, will deal with all aspects of malacology of the Near East. Contributions will be published in *Argamon*, the journal of the Israel Malacological Society. Further information can be obtained from the Secretary, Israel Malacological Society, P.O. Box 9216, Haifa, Israel.

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DEUTSCHE MALAKOZOOLOGISCHE GESELLSCHAFT, ANNUAL MEETING. — The annual meeting in 1972 of the Deutsche Malakozoologische Gesellschaft (German Malacological Society) was held at Braunau/Inn (Austria) on 11-14 May, together with the Zoologische Gesellschaft Braunau (Zoological Society Braunau). The 1972 ordinary assembly of members of the Deutsche Malakozoologische Gesellschaft was held at this meeting in the evening of 13 May. Inquiries may be sent to Mr. Fritz Seidle jun., Zoolog. Ges. Braunau, Firscher-Gasse 4, A-5280 Braunau/Inn, Austria. The program of the meeting is given below.

Vorläufiges Programm

Donnerstag, 11 Mai 1972 (Chr. Himmelfahrt)

Vormittags: Eintreffen der Teilnehmer.

Nachmittags (15 Uhr): Exkursion zum Innufer in Braunau (*Bythinella austriaca austriaca, Ena montana, Oxychilus mortilleti, Clausilia dubia obsoleta, Zenobiella umbrosa, Trichia edentula subleucozona, T. unidentata unidentata, T. u. subalpestris* usw.). Führung: W. Wiesinger.

Abends (19 Uhr): Empfang des Bürgermeisters der Stadt Braunau am Inn, Dr. Fuchs.

Freitag, 12 Mai 1972

Vormittags (9 Uhr): Besichtigung der Stadt. Führung: Stadtrat Raschhofer (allgemeiner Teil), Dr. Fink (historischer Teil) und Stadtbaudirektor Arch. Dipl.-Ing. Reinisch (das neue Braunau).

Nachmittags (13 Uhr): Exkursion nach Ranshofen (kurze Besichtigung der prächtigen Barockkirche; anschliessend Aufsammlung von diversen Arten, z.B. *Discus perspectivus, Oxychilus mortilleti, Clausilia dubia obsoleta, Iphigena plicatula grossa, Iphigena ventricosa* usw.). Weiterfahrt nach Unterrothenbuch (zahlreiche Arten, z.B. *Cochlicopa nitens, Discus perspectivus, Clausilia pumila, Perforatella bidentata, Trichia edentula subleucozona* usw.), Oberrothenbuch (Blick auf das Inntal und das ornithologisch interessante Mündungsdelta der Salzach; Aufsammlung von diversen Arten, z. B. *Acicula polita, Pagodulina pagodula principalis, Discus perspectivus, Vitrea subrimata, Clausilia dubia obsoleta* usw.) und Ach an der Salzach (einzigartiger Blick auf die alte bayerische Herzogstadt Burghausen mit der grössten Burganlage Deutschlands). Ornithologische Führung: Dr. J. Reichholf.

Abends (19 Uhr): Vorträge, Diskussionen. Dkfm. Dr. Krisai: "Die Pflanzendecke des unteren Inntales"; Dr. J. Reichholf: "Die Fauna des unteren Salzach- und Inntales".

Samstag, 13 Mai 1972

Vormittags (9 Uhr): Exkursion in die Auen am westlichen stadtrand von Braunau (*Viviparus contectus, Anisus vortex, Hippeutis complanatus, Planorbarius corneus, Ena montana, Clausilia pumila, Iphigena plicatula grossa, Zenobiella umbrosa, Perforatella bidentata, Trichia edentula subleucozona, Trichia unidentata unidentata, T. u. subalpestris* usw.).

Nachmittags (13 Uhr): Exkursion nach Obernberg (Blick auf das Inntal mit den Kraftwerksanlagen, kurze Besichtigung des malerischen Marktplatzes), zum Jakobsbrünnl (zahlreiche Arten, z.B. *Aegopis verticillus, Clausilia pumila* usw.), nach Minaberg (zahlreiche Arten, z. B. *Acicula sublineata, Aegopis verticillus, Clausilia pumila, Iphigena plicatula grossa, Ruthenica filograna* usw.; Blick über eines der bedeutendsten Wasservogelbrutgebiete nördlich der Alpen /Taucher, Reiher, Enten/) und nach Reichersberg (kurze Besichtigung des sehenswerten Stiftes, Möglichkeit zum Besuch des Museums). Ornithologische Führung: Dr. J. Reichholf.

Abends (20 Uhr): Ordentliche Mitgliederversammlung der DMG. Anschliessend Lichtbilder von früheren Tagungen und Treffen (Wir bitten die Teilnehmer, Dias mitzubringen!). Ausser Programm, aber ohne zusätzlichen Zeitaufwand, können an diesem Tag noch etwa 50-60 Molluskenarten gesammelt werden (u.a. *Gyraulus acronicus, Vertigo alpestris, Vertigo angustior, Vertigo heldi, Vallonia declivis* usw.).

Tagesordnung der Ordentlichen Mitgliederversammlung 1972:

1. Bericht des Vorstandes
2. Entlastung des Vorstandes
3. Wahl des neuen Vorstandes
4. Bestimmung des Ortes der nächsten Mitgliederversammlung (1975) gem. § Abs. 2 der Satzung
5. Verschiedenes

Sonntag, 14 Mai 1972

Vormittags (9 Uhr): Exkursion zum Naturschutzgebiet "Hagenauer Bucht" (Wasservogelbrutgebiet und Schmetterlinge) und in die Reickersdorfer Auen (zahlreiche Arten, z.B. *Bythinella austriaca cylindrica, Hippeutis complanatus, Ancylus fluviatilis, Clausilia pumila, Zenobiella umbrosa, Iphigena plicatula grossa, Perforatella bidentata, Trichia edentula subleucozona, T. unidentata unidentata, T. u. subalpestris* usw.). Ornithologische Führung: Dr. J. Reichholf.

Nachmittags (14 Uhr): Exkursion in die Auen am Simbacher Baggersee (zahlreiche Arten, z.B. *Clausilia pumila, Perforatella bidentata, Trichia edentula subleucozona* usw.).

Abends (20 Uhr): Gemütlicher Abschiedsabend mit Tanz im Café Reicheneder ("Dancing 57"), Braunau, Stadtplatz 57.

CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND, ANNUAL GENERAL MEETING. — The Annual General Meeting of the Conchological Society was held on 28 February 1972 in London, England, U.K., at the premises of the Linnean Society of London in Burlington House, Piccadilly. Membership now

stands at 492, with members drawn from most countries of the world. Mr. T. Pain, the President delivered his Presidential Address entitled "Origin & distribution of non-marine Mollusca in South America." The following officers were elected for the year 1972-73: President — T. E. Crowley; Hon. Secretary — Mrs. E. B. Rands; Hon. Treasurer — Mrs. M. Fogan; Hon. Editor — Mrs. N. F. McMillan; Non-marine Recorder — Dr. M. P. Kerney; Marine Recorder — Mrs. S. M. Turk.

NETHERLANDS MALACOLOGICAL SOCIETY. — The Hon. Secretary's Report for the year 1971 shows that the Society has a total of 416 members, of which a fair number consists of foreigners. The Society publishes a mimeographed newsletter, sent to all members free of charge. In the period 1934-71 a total of 145 issues of the newsletter have appeared at irregular intervals with a maximum of 6 per annum. This newsletter contains items about the Society and its meetings, reports on field trips, and short papers, frequently of faunistic interest. The newsletter is wholly in Dutch and is being indexed every decade or so, so that the information is easily retrieved. The Society also publishes its scientific journal *Basteria*, which was started in 1936. In 1971 Vol. 35 was published with a total of 133 pages. The number of pages per volume (6 numbers in 1 volume per annum; numbers are usually combined) varies nowadays from 100-154; the journal is produced by and at the expense of the Society and is almost wholly paid for by the subscribers (348 among the members of the Society and 81 others; furthermore 36 copies are sent in exchange to libraries, museums, universities, etc.). From the beginning the journal has been somewhat international in scope, which is shown by the 1971 papers (of the 16 papers, 8 were in Dutch, 6 in English and 2 in German; of the 15 authors, 5 resided outside the Netherlands). All papers in Dutch have summaries in English. Every 4 or 5 years the contents are fully indexed. Much to our satisfaction *Basteria* is available in most countries and in the main centres of scientific research; the number printed is now 520. There is a stock of old volumes still available for sale or exchange. Reprints of most papers are also still for sale for a nominal charge. Foreign members of the Society may use *Basteria* as medium for their publications; non-members may publish papers provided modest page charges are paid. The Editor-in-Chief is Dr. A. C. van Bruggen, Department of Systematic Zoology of the University, c/o Rijksmuseum van Natuurlijke Historie, Raamsteeg 2, Leiden, Holland.

The Society has an interesting library for its members. This library consists of a limited number of books, a large number of reprints and pamphlets, and series of journals obtained in exchange for *Basteria* and/or the newsletter. Some of these are unique in the Netherlands. The contents of the library are available for inter-library loans throughout the country, although members of the Society have preference in dealing with the library.

The Society usually organizes 2 field meetings per annum. Additionally, scientific meetings are held in Spring and Winter, during which lectures, short communications and exhibits are presented. There are local sections of the Society in the cities of The Hague, Amsterdam and Rotterdam. These are small numbers of local members of the Society who hold their own meetings open to all other members.

Those interested in the Society or *Basteria* should contact the Hon. Secretary, Nederlandse Malacologische Vereniging, c/o Rijksmuseum van Natuurlijke Historie, Raamsteeg 2, Leiden, Holland.

UNITAS MALACOLOGICA EUROPAEA, NEW COUNCIL. — At the general Assembly which took place during the Fourth European Malacological Congress in September 1971, the Council for the period 1971-74 was elected.

President, Dr. Ferdinando Toffoletto, Museo Civico di Storia Naturale, Corso Venezia, 55, I-20121 Milano, Italy.

Vice-president, Dr. A. C. van Bruggen, Afdeling Systematische Dierkunde, Rijksmuseum van Natuurlijke Historie, Raamsteeg 2, Leiden, Holland.

Secretary, Dr. O. E. Paget, Naturhistorisches Museum, Burgring 7, A-1014 Wien, Austria.

Treasurer, Dr. P. Jung, Naturhistorisches Museum, Augustinergasse 2, CH-4051 Basel, Switzerland.

Member of Council, J. F. Peake, B. Sc., British Museum (Natural History), Cromwell Road, London, S.W.7, England.

The Fifth European Malacological Congress is to take place in Milan, Italy, in 1974.

WESTERN SOCIETY OF MALACOLOGISTS. — The Fourth Annual Meeting of the Western Society of Malacologists was held 16-19 June 1971 at Asilomar, Pacific Grove, California, U.S.A. Dr. Eugene Coan of Palo Alto, the President of the Society, presided. Thirty six papers on a variety of topics were presented, including a symposium on opistobranchs and one on the evolution of the muricacean gastropods in time and space. Eight exhibits including 3 new books near publication by members were displayed. The banquet speaker was Dr. T. A. Abbott of the Delaware Museum of Natural History, who also showed a movie entitled "The makings of a malacologist." Abstracts, summaries and reports appeared in *The Echo*, the annual publication of the Society.

SOCIÉTÉ FRANÇAISE DE MALACOLOGIE. — Association fondée en 1961 et régie par la Loi de 1901. Siège social: 55 rue Buffon, Paris 5ème, France.

La Société Française de Malacologie a été fondée le 29 Janvier 1969. Elle a pour but d'encourager et de développer toutes études concernant les Mollusques actuels et fossiles, de faciliter les relations entre les malacologistes et de les documenter sur les recherches en cours dans les différents laboratoires de France et d'autres pays.

Activites. La Société organise de congrès, suscite des colloques et favorise l'activité de groupes de travail. Son premier congrès s'est tenu à Caen en Septembre 1970. Deux colloques sont prévus en 1972. Une "Commission Faunistique Continentale", créée en 1970, a entrepris l'inventaire et la répartition géographique des Mollusques continentaux actuels en France. Les compte-rendus des communications aux congrès et les rapports des colloques sont publiés dans la revue *Haliotis* de la Société. Les auteurs de communications aux congrès et les rapporteurs aux colloques doivent être membres de la Société.

Publications. Chaque membre de la Société reçoit, outre la revie *Haliotis*, des circulaires d'informations et une liste de tous les travaux malacologiques reçues au Siège Social au cours de chaque trimestre (quatre circulaires bibliographiques dans l'année). La "Commission Faunistique Continentale" publie des documents de travail qui sont diffusés à tout membre en ayant fait la demande au Secrétariat.

Adhesion et cotisation. Les demandes d'adhésion sont ratifiées par le Conseil d'Administration; aucune condition particulière n'est exigée pour être membre, personne physique ou personne morale. Le montant annuel de la cotisation est de 35 francs pour les personnes physiques (25 francs pour les étudiants et de 50 francs pour les laboratoires, musées, sociétés, bibliothèques etc. .) La cotisation donne droit au volume d'*Haliotis* de l'année. Le volume I (no. 1 et 2) d'*Haliotis*, publié en 1971, est vendu au pris de 50 francs, "l'Annuaire des Membres de la Société" (paru en 1970) au prix de 10 francs. Les cotisations et les commandes de publications sont payables, de préférence par chèque postal ou par mandat, à l'ordre de la Société Française de Malacologie, 55 rue de Buffon, Paris 5ème (C.C.P. 30 387.66 - La Source). Les chèques bancaires devront être adressés directement au Trésorier de la Société (adresse ci-après).

L'association est dirigée par un Conseil d'Administration de 12 membres, élus pour trois années par l'Assemblée générale ordinaire. Le Conseil est renouvelable par tiers chaque année, les membres sortants étant rééligibles. Le Conseil élit, en son sein, pour une durée de un an, un Bureau composé d'un président d'un vice-président, d'un secrétaire général, d'un secrétaire adjoint et d'un trésorier. Le Conseil invite chaque année à ses séances quatre membres de la Société de nationalité non française. La Société compte 200 adhérents au 1er Janvier 1972.

Composition du Conseil d'Administration pour l'exercice 1971-72. President, B. Salvat, Laboratoire de Biologie Marine (E.P.H.E.), 55, rue Buffon, Paris 5 ; Vice-Président, W. Streif, Laboratoire de Zoologie, Faculté des Sciences, 14-Caen; Secrètaire-général, J.C. Fischer, Laboratoire de Paléontologie (Muséum) 8, rue de Buffon, Paris 5 ; Secrétaire-Adjoint, H. Chevallier, Dept. de Malacologie (Muséum), 55, rue de Buffon, Paris 5 ; Trésorier, P. le Gall, Laboratoire de Biologie Marine, 14 - Luc-Sur-Mer; Conseil, P. Lubet (Caen), A. Lucas (Brest), J. Ripplinger (Besançon), J. Tardi (La Rochelle), Mme G. Termier (Paris), G. Truc (Lyon), J. Vovelle (Paris); Membres étrangers invités à siéger au Conseil pour l'année 1972, J. B. Burch (U.S.A.), A. Girod (Italie), J. Kriz (Tchécoslovaquie), J. J. van Mol (Belqique).

SECOND ANNUAL SYMPOSIUM OF THE ISRAEL MALACOLOGICAL SOCIETY. — The Second Annual Symposium took place on 2 April 1972 at Nahariya, Israel. The occasion was marked by the inauguration of the Malacological Section of the Nahariya Museum. The Proceedings of the Symposium will be published in *Argamon*, the journal of the Israel Malacological Society.

SOCIÉTÉ BELGE DE MALACOLOGIE. — On 29 January 1972, the general assembly of the members of the "Association belge de Malacologie, de Conchyliologie et de Paléontologie" decided to resolve themselves into a non-profit association called the "Société belge de malacologie."

The new Society will go on with the activities of the former Association, but will do so with new scientific fervor, and by especially enlisting younger members. The Society expects to encourage scientific research, such as cooperating with the European Invertebrate Survey, and especially to promote protection of the natural environment.

ANNOUNCEMENTS

* * * * * * *

HALIOTIS, A NEW MALACOLOGY JOURNAL. — During 1971, the Société Française de Malacologie began publishing their new journal, *Haliotis*. Vol. 1, No. 1 contains all papers read at the Society's first national Congress held in Caen in September, 1970. Vol. 1, No. 2 contains reports of the 2 colloquies which took place simultaneously with the Congress, "Sexuality of mollusks" and "Ecology and paléoecology of mollusks."

This new publication, which was originally to be called "*Actes de la Société Française de Malacologie*," is provided free of charge to members of the Society.

Contents of *Haliotis*, Vol. 1 (1971), are given on p 78 - 80 of this issue of *Malacological Review*.

SUPPLEMENTS TO *MALACOLOGICAL REVIEW*, VOLUMES 4 AND 5. — The previously announced supplement to Vol. 4 will not be published by *Malacological Review*. The supplement to Vol. 5, *The freshwater mollusks of Taiwan* (*Formosa*), will be published as scheduled. The price of the latter is US$ 15.00, A$ 13.50 or ¥ 5400 (postpaid), and may be ordered from our American, Australian or Japanese editorial offices.

PUBLICATION SCHEDULE FOR *MALACOLOGICAL REVIEW*. — Beginning with Vol. 6 (1973), new issues of *Malacological Review* will be scheduled for publication and mailing in January (1st issue for the calendar year) and July (2nd issue for the calendar year).

THE INTERNATIONAL MUSEUM OF MALACOLOGY, NICE, FRANCE. — This museum, located at 3, Cours Saleya, Nice, is a private creation presenting symbiosis of art and science. Carefully selected shell collections reveal a world of fantasy by the beauty of their shapes and colors. It is a constantly changing museum, continually progressing, with many innovations following visitors' suggestions.

The museum consists of 2 rooms open to the public. The 1st contains exotic species and the 2nd contains Mediterranean shells. An aquarium for research purposes allows the observation of living animals in simulated natural environment. A lithography press dating from Daumier's day, with its huge wheel, recalls the technical processes once used for illustrating works of conchology. On the walls are artistic photographs of shells by Denise Valêro.

GRADUATE STUDY IN MALACOLOGY AT THE UNIVERSITY OF MICHIGAN. - National Institutes of Health Predoctoral Traineeships in malacology are available at the Museum and Department of Zoology, The University of Michigan, to qualified U.S. citizens. Participants are expected to pursue graduate studies leading to the Doctor of Philosophy (Ph.D.) degree in Zoology. Active research programs dealing with mollusks include cytology, cytogenetics, cytotaxonomy, genetics, cell, tissue and organ culture, developmental biology, comparative physiology and biochemistry, systematics, natural history, ecology, zoogeography, parasitology and medical zoology. Special emphasis is placed on freshwater mollusks, although aspects of land and marine malacology are also considered. Facilities include well-equipped modern research laboratories for various aspects of biological research. First year stipends are US$ 2400 plus tuition, plus a US$ 500 allowance for each dependent. Address inquiries to the Mollusk Division, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48104, U.S.A.

William Charles Starrett
1912–1971

Malacological Review, 1972, 5: 40-41

OBITUARY
WILLIAM CHARLES STARRETT
1912-1971

Dr. William Charles Starrett, river biologist with the Illinois Natural History Survey since July 1, 1948, died December 29, 1971 at Havana, Illinois, U.S.A. Dr. Starrett was a native of Pekin, Illinois. He earned bachelor's and masters' degrees at the University of Illinois, and he received the Ph.D. degree from Iowa State College in 1948. He served in the U. S. Navy during World War II in the European, African and Pacific theatres. He married Irene Jensen of Audubon, Iowa in 1948.

Dr. Starrett was hired by the Illinois Natural History Survey to replace Paul G. Barnickol, who, operating from the Survey's laboratory boat *Anax*, had completed a cooperative field investigation with the states of Missouri and Iowa on the fishes of the Mississippi River. Dr. Starrett's first assignment was to work up these data, which resulted in 2 Illinois Natural History Survey bulletins, "Commercial and Sport Fishes of the Mississippi River Between Caruthersville, Missouri and Dubuque, Iowa" (1951) and "Efficiency and Selectivity of Commercial Fishing Devices Used on the Mississippi River" (1955).

Dr. Starrett was greatly interested in the Illinois River and the changes that had taken place in its fauna as a result of varying degrees of pollution since 1900. These changes were defined in the Illinois Natural History Survey publications "Man's Effect on the Fish and Wildlife of the Illinois River" (1966, with H. B. Mills & Frank C. Bellrose), and "A Survey of the Mussels (Unionacea) of the Illinois River: a Polluted Stream" (1971). His final scientific contribution, entitled "Man and the Illinois River", was presented to the International Symposium on Rivers held at Amherst College in June, 1971.

In addition to his above publications which involved mollusks, Dr. Starrett published many scientific papers on fishes and birds. He was a member of the Midwest Benthological Society, American Fisheries Society, Upper Mississippi River Conservation Committee and American Society of Limnology and Oceanography. He was given a special citation in 1971 as part of the State of Illinois Governor's Awards Program.

Dr. Starrett was on friendly terms with many people having an interest in the Illinois River — malacologists, fisheries biologists, commercial fishermen, civil servants and private administrators. He was a meticulous researcher and will long be remembered for his contributions to Illinois River biology.

Leo George Hertlein
1898–1972

Malacological Review, 1972, 5: 42-43

OBITUARY
LEO GEORGE HERTLEIN
1898-1972

Dr. Leo George Hertlein, Curator Emeritus of Geology, California Academy of Sciences, San Francisco, died on January 15 after a brief illness. Born in Pratt, Kansas in 1898, he took his A.B. from the University of Oregon in 1922, and received his graduate degrees from Stanford University (A.M., 1923; Ph.D., 1929). He was employed at the academy from 1925 until his retirement in 1970, at which time he was the senior member of the staff. Since then he had continued his research program, and at the present time an important and major contribution by Dr. Hertlein to the knowledge of paleontology of Southern California is in press as a *Memoir* of the San Diego Society of Natural History.

Dr. Hertlein was universally esteemed among his scientific colleagues. He was author or coauthor of more than 150 scientific papers, many of them of monographic scope. On leaves from the Academy, he did paleontological research for various oil companies and the United States Geological Survey. He participated in Academy expeditions, including work in the Galapagos islands.

Dr. Hertlein and his scientific contributions were specially recognized in 1970 by a number of *The Nautilus* (Vol. 84, No. 2, October) being issued in his honor. A more detailed biographical sketch and a complete bibliography of Dr. Hertlein are included in that issue.

Andor Horváth
1913–1972

Malacological Review, 1972, 5: 44-45

OBITUARY
ANDOR HORVÁTH
1913-1972

Dr. Andor Horváth died suddenly on the morning of 8 February 1972, on his way to work in the Department of Zoology of Szeged University. We had lost an untiring teacher of several generations and an internationally recognized scholar of malacology.

The greater part of his life was spent in Szeged, Hungary, a university town lying on the Tisza River. Here he studied, and here he became a secondary-school teacher of biology and geography, and later assistant lecturer, lecturer and assistant professor at the University. Here, too, he obtained his doctorate and next the degree of Candidate of Science.

He was a born malacologist, who from his early youth resolutely unearthed the fauna and ecology of the shellfish and snails of the Szeged district, and then material from other parts of Hungary and from all over the world, both Recent and Pleistocene species alike. From the material available he was outstandingly able in characterizing not only the surface regions, but also the Pleistocene layers as well. His quantitative and qualitative results obtained with his reconstruction model made a serious contribution in the fields of zoology and palaeontology.

His knowledge of the entire animal kingdom was prodigious, and he was thus always able to tackle a problem with certainty, to render assistance to his students and colleagues, and to provide special advice in questions of agricultural practice.

He was a completely reliable member of the Department and of his profession. In his roles as Editor and Co-editor, respectively, he provided a considerable stimulus to the journals *Acta Biologica Szegediensis* and *Tiscia*. He was a founding member of a number of Hungarian scientific societies, as well as the Unitas Malacologica Europaea.

Dr. Horváth's memory is preserved in some 35 scientific papers, in his very large collection of Hungarian and foreign mollusks, by his friends, by his colleagues, and by the young generation to whom he passed on with such great expertness his systematic, ecological, zoogeographical and malacological knowledge, and his research accomplishments.

BOOK REVIEWS

PROCEEDINGS OF THE SYMPOSIUM ON MOLLUSCA HELD AT COCHIN FROM JANUARY 12 *TO* 16, 1968. Marine Biological Association of India, Marine Fisheries P.O., Mandapam Camp, India. Symposium Series 3. Part 1, p i-xxxv, 1-385, 1968. Part 2, p i-iv, 387-706, 1969. Part 3, p i-iv, 707-1052, 1970.

The Marine Biological Association of India sponsored an international "Symposium on Mollusca" at Cochin, Kerala State, India, from 12 to 16 January 1968. The meetings were nicely organized and extremely well run. Unfortunately, there were only 14 foreign scientists of the 134 registered participants, and it was obvious that the symposium suffered from lack of personal participation of many of the world's leading malacologists. Contrary to the preface of Part I of the *Proceedings*, the response from the eminent malacologists all over the world was not great. The lack of foreign participation may perhaps be partly attributed to the fact that the Third European Malacological Congress was held only a few months before (September 1967) in Vienna.

Eight countries were represented at the Cochin gathering. The number of papers published in the *Proceedings* from each country is given in Table 1. The topics represented in the 3 volumes are given in Table 2, along with the number of papers in each of 16 categories. As can be seen in Table 1, the papers published in the *Proceedings* have little to do with papers presented at Cochin. For example, there were 6 participants from the United States, but there are 25 U.S.A. papers in the *Proceedings*. A long session at the meetings dealt with boring and fouling mollusks, but only 8 papers on the topic can be found in the *Proceedings*.

Systematics and faunal lists account for 76% of the papers in Part 1, while 88% of the papers in Part 2 deal with ecology, distribution and physiology-biochemistry. Part 3 primarily deals with commercial aspects, including boring mollusks and the molluscan fisheries industry. Taken as a whole, the 3 volumes and 95 papers are rather uninspiring. Papers range from extremely poor to excellent. There are preliminary studies and review papers of 2 or 3 pages scarcely covering vintage literature and hardly scratching the surface of recent findings. One author in Part 2 "contributed" 4 times without adding substance to the *Proceedings*. About 20% of the papers have little if any value. There are several excellent reviews and several valuable research papers which, together, do not exceed 25% of the contributions. The greatest value in the 3-part series is the concentration of papers on the commercial aspects of mollusks found in Part 3. As such, the editors should have reduced the contents to 2 volumes.

The quality of the printing is exceedingly poor. The plates reproduced terribly. The editing was not uniform, e.g., full article titles were given in the references for some papers, and not in others (Parts 2 and 3). With all factors considered, the *Proceedings* reviewed here certainly do not represent a milestone in the history of malacological publications, but there are some valuable contributions which justify the addition of these 3 volumes to the library shelf.

These *Proceedings* clearly show that it is inadvisable to attempt to run a first-class symposium by open invitation and blind acceptance of all papers. It is more advisable to structure the content and give selective invitation to obtain high-powered manuscripts. Only first-class papers should be accepted, and "padding" for bulk with third-class attempts should be avoided at all costs.

TABLE 1. A tabulation of international participation at the Symposium on Mollusca and contributions to the *Proceedings*.

Country	Participants Present	Contributors to Part 1	Contributors to Part 2	Contributors to Part 3
Australia	0	1	1	2
Austria	1	2	0	0
Canada	1	1	0	0
Ceylon	2	1	2	1
Cuba	0	0	0	1
England	1	1	2	1
France	0	0	0	1
Germany	0	0	0	2
Greece	0	0	0	1
India	120	7	15	13
Italy	0	0	3	0
Japan	0	0	0	2
Netherlands	0	0	0	2
Scotland	2	0	1	2
Singapore	0	1	0	0
Spain	0	0	0	1
USA	6	10	8	7
USSR	1	1	1	0
Wales	0	0	0	1
TOTAL	134	25	33	37

TABLE 2. Categories of papers published in the *Proceedings of the Symposium on Mollusca*

Topics	Part 1	Part 2	Part 3
Anatomy (systematics)	2	0	0
Biochemistry	0	3	0
Boring and Fouling	1	0	7
Cellular Defense	0	1	0
Commercial (fisheries industry)	0	1	23
Cytology	1	3	0
Ecology-Distribution	2	7	0
Faunal Lists	9	0	0
Histochemistry	0	1	0
Historical	0	0	1
Neurosecretion	0	1	0
Ontogeny	0	7	0
Parasitology	0	0	4
Physiology-function	2	5	1
Radiobiology	0	4	0
Systematics (& life history)	8	0	1

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U. S. A.

SEA SHELLS OF THE TEXAS COAST. Andrews, Jean. University of Texas Press, Austin, Texas, U.S.A. 1971. 298 p. US$ 17.50.

Upon seeing the cover of this book on my desk, one of my distinguished malacologist friends said, "Just what we don't need, another 'Oh My' shell book!" I rose to the defense because this book differs from the usual shell guide in the high standard of scholarship and the quality of presentation.

My first view of the sea shore was in Texas and my first serious attempt to identify marine molluscs was made on animals collected there. I remember well the frustrations in finding shells which were not in any of the field guides available at the time, and I found that much of the literature needed for identification was not readily available. This work should ease the frustrations of both serious students and collectors, and it may even inspire the curious youth into a career in malacology.

The 2 most valuable features of this volume are the presentation of more than 350 excellent black-and-white photographs and the inclusion of many minute species for the first time in popular literature.

The short historical chapter sets the scene for the author's description of the major physical features of the Gulf of Mexico and the Texas coast. These descriptions are supplemented by maps and specific directions to good collecting localities. General procedures are outlined for collecting and preparing specimens, as well as for recording essential data. Specific information is given for the Texas coast, including safety precautions readily appreciated by all who have collected there.

Other valuable features of this volume include short accounts of early naturalists responsible for naming more than half of the Texas marine molluscs, a short explanation of scientific nomenclature, and a description of intertidal organisms often associated with the molluscs. The author includes a short description of the photographic techniques used in the preparation of her photographs, and she even provides the reader with a list of local shell clubs and of museums with extensive collections of molluscs.

Each species considered in the text is shown photographically. All illustrations are essentially the same size regardless of the actual size of the shell, which is given in the description. The systematically arranged species descriptions include not only the scientific names, but their derivations, original citations and the common names. The color, shape, markings, sculpture, aperature characteristics and the nature of the periostracum are presented for each species. The specific habitats for each species are described, as well as the general geographic and geologic ranges and good collecting localities. There are even some interesting recipes given for bivalves.

This volume is relatively free from typographical and production errors. The sizes of small shells are given in mm, while those of larger ones are given in inches. This is confusing and undesirable in a scientific work.

The section on marine aquaria should have called attention to *Instant Ocean* (Aquarium Systems, Inc., Wickliffe, Ohio, U.S.A.), which is more economical and actually better for enclosed systems than most sea water. Also omitted from this section is the use of oyster shell, available from local feed stores, an inexpensive, but excellent filtering and buffering material that is routinely used in inland laboratories.

The book contains few generalities with which I would disagree. However, the statement that, "The winter months appear to be the usual time for depositing eggs" is not valid either in a general sense or in the Gulf of Mexico. Limitations

of space often force such generalizations. None the less, the author has handled most of the subject in truly superior style, and difficult groups such as the pyramidellids are dealt with especially well considering the lack of precise information.

This is an excellent book and will be valued by all who work with molluscs in the Gulf of Mexico. The author deserves the admiration of all malacologists for the high standards she has set; she has established a new level of quality for such works in the future. The author's enthusiastic account should serve to stimulate all readers to gain first-hand experience with these fascinating marine molluscs.

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Malacological Review, 1972, 5: 51-53

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(Continued from Vol. 4)

At the time MALACOLOGICAL REVIEW, Vol. 4, No. 2 went to press all issues for 1970 of some of the journals had not yet been received at our editorial offices. The tables of contents of these late numbers are included here.

VENUS
THE JAPANESE JOURNAL OF MALACOLOGY

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COMUNICACIONES
DE LA
Sociedad Malacológica
DEL
Uruguay

MONTEVIDEO URUGUAY

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LAVORI
della
Società Malacologica Italiana

SOCIETÀ MALACOLOGICA ITALIANA

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[3]Footnotes 4-23 list the main editorial offices of the various journals.
[4]18/55 Prince Albert St., Mosman, N.S.W. 2088, Australia.
[5]Senckenbergishchen Naturforeschende Gesellschaft, Senckenberg-Anlage 25, 6 Frankfurt 1, Germany (FR).
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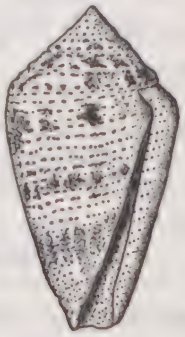

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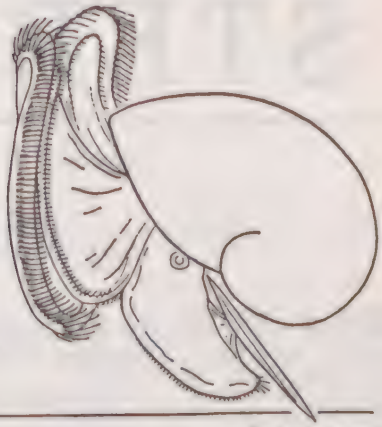

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BY

EUGENE V. COAN

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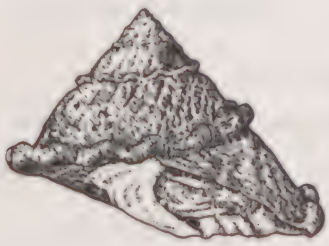

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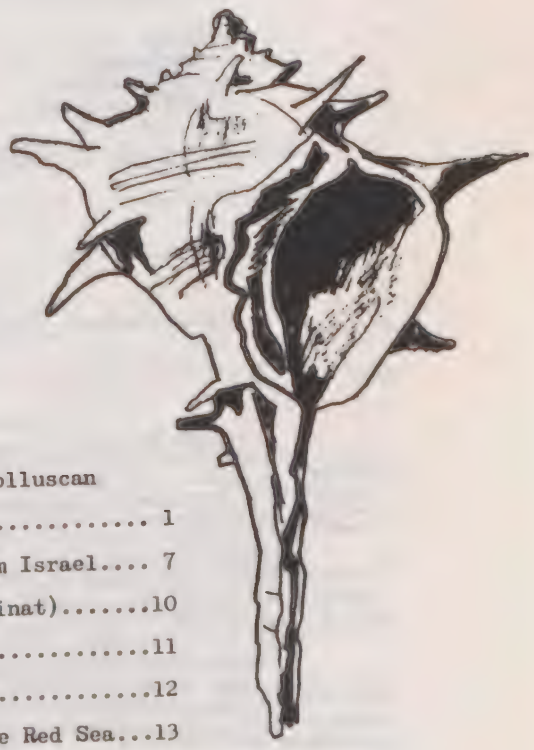

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HALIOTIS

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La Société Française de Malacologie a été fondée le 29 janvier 1969. Elle a pour but d'encourager et de développer toute étude concernant les Mollusques actuels et fossiles, de faciliter les relations entre les malacologistes et de les documenter sur les recherches en cours dans les différents laboratoires de France ou d'autres pays. L'association est dirigée par un Conseil d'Administration de douze membres élus pour trois années par l'Assemblée Générale ordinaire.

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Chaque membre de la Société reçoit des circulaires d'informations ronéotées ainsi que la revue "HALIOTIS" éditée par la Société. Parmi les circulaires, l'information bibliographique est diffusée aux membres par une liste de tous les travaux malacologiques reçus au Siège Social au cours de chaque trimestre (quatre circulaires bibliographiques dans l'année).

Toutes demandes, d'adhésion ou de renseignements, doivent être adressées au Secrétariat de la Société.

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Le Gérant : Albert LUCAS

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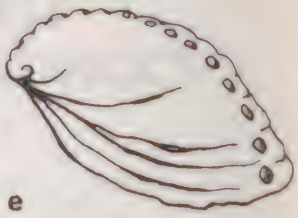

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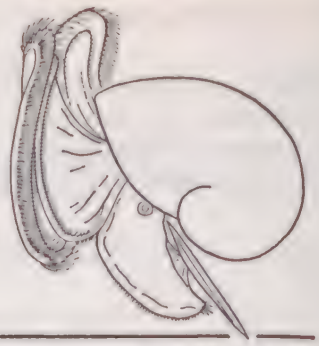

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ANNOUNCEMENT - FORMATION OF COUNCIL OF SYSTEMATIC MALACOLOGISTS

On November 16th and 17th, 1972, malacologists representing many of the major molluscan collections in North America met in Philadelphia, Pennsylvania, U.S.A. As a result of this meeting, it was decided to form a "Council of Systematic Malacologists" as outlined in the following resolution. As indicated in this resolution, working groups are attempting to develop statements in areas of concern to malacologists in a much broader sense than just the curatorial community. At present this is a group without membership rolls, dues, constitution or bylaws, but its members share an interest in and concern for both malacology as a science and the systematic resources that are basic to molluscan research. Another meeting is scheduled for early April in Chicago. Those wishing further information should contact Dr. Alan Solem, Acting Chairman, Council of Systematic Malacologists, c/o Field Museum of Natural History, Chicago, Illinois 60605, U.S.A.

Resolution

Whereas the Phylum Mollusca is exceeded in living diversity only by the Phylum Arthropoda and flowering plants;

Whereas the existing collections of mollusks in North American museums number between 25,000,000 and 40,000,000 specimens;

Whereas the management of these collections presents problems that are not shared with collections of other phyla;

Whereas the services of malacology to society can be improved through definition of goals and priorities in malacological research and collection management;

The undersigned systematists, representing major malacological collections in North America, have organized a "Council of Systematic Malacologists."

The purposes of this organization shall be:

1) To prepare recommendations concerning standards and techniques of collection management for malacological resources;
2) To define the goals and priorities of malacology.

Membership shall be open to all professional persons in the Americas who use or manage systematic malacological resources. Membership shall be expanded through announcements in specialist journals and at relevant meetings.

Periodic meetings shall be held in adjunct with scheduled scientific meetings or as needed to confer on common problems.

A temporary steering committee has been formed to organize and promote an effective representative group for malacology in the Americas. This committee consists of:

Alan Solem, Chairman
Arthur H. Clarke
George M. Davis
James H. McLean

Working subgroups have been appointed to prepare recommendations concerning:

1) Compatible electronic data processing and curatorial programs for use by malacologists in collection management and research;
2) Articulation of national goals for malacological research;
3) Coordination of specimen acquisition policies for malacological collections;
4) Preparation of position papers outlining priority programs for malacology.

Preliminary reports shall be circulated to the undersigned and other interested parties prior to a formal meeting open to wide participation by malacologists.

Signed,

R. Tucker Abbott, *Delaware Museum of Natural History*

Kenneth J. Boss, *Museum of Comparative Zoology, Harvard University*

J. B. Burch, *Museum of Zoology, The University of Michigan*

Arthur H. Clarke, *National Museum of Natural Sciences, National Museums of Canada*

George M. Davis, *Academy of Natural Sciences of Philadelphia*

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Malacological Review , 1972, 5: 95-164

COMPARATIVE STUDIES ON A POLYPLOID SERIES OF THE AFRICAN SNAIL GENUS *BULINUS* (BASOMMATOPHORA: PLANORBIDAE)[1,2]

Shi-Kuei Wu

ABSTRACT

African freshwater bulinine snails are remarkable in that they include polyploid species. They are also of medical importance because some of their members serve as intermediate hosts of the human trematode parasite *Schistosoma haematobium*.

Most species of *Bulinus* are similar in morphology, and especially those constituting the traditional "subgenus" *Bulinus*, i.e., the *truncatus* and *tropicus* groups. The purpose of this study was to determine whether any morphological distinction could be made between members of the diploid-polyploid series in these groups, and to see how these differences, if any, would correlate with cytological, parasitological, biochemical and serological data known or to be yet determined. Cross-breeding experiments were attempted in order to study the degree of genetic continuity between diploid and polyploid populations.

Four cytologically distinct and geographically separated populations were used for the comparative morphological study: population I (*Bulinus tropicus*, n=18, 2n=36, diploid) from South Africa; population II (*Bulinus truncatus*, n=36, 2n=72, tetraploid) from Egypt; population III (*Bulinus hexaploidus*, n=54, 2n=108, hexaploid) and population IV (*Bulinus octoploidus*, n=72, 2n=144, octoploid) both from Ethiopia.

Within the same population shell characters were relatively uniform for laboratory-bred as well as field-collected specimens. The growth changes of the shell were mainly in the spire length as expressed in the shell length/aperture length (L/AL) ratio. Population I and II were relatively high-spired (mean L/AL 1.54 and 1.53), while populations III and IV were medium-spired (mean L/AL 1.40 and 1.39). On the other hand, the average shell shape of populations I and III was more slender and less globose than that of populations II and IV.

Similarly populations I and III had darkly pigmented animals with black mantle markings and black pigment on the tunica propria overlying the visceral hump, whereas populations II and IV had lightly pigmented animals and no black pigment in the mantle.

To facilitate future comparisons of radulae it is proposed that descriptions should cover half a transverse radular row situated about 30±5 rows from the most anterior rachidian tooth, viewed from a definite, arbitrarily determined angle. Descriptions should not only account for the mesocone of the 1st lateral tooth, but also for the shape and size of the ectocones and

---

[1]Adapted from a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Michigan, December 1971.

[2]This investigation was supported by a research grant (AI 07279) from the National Institute of Allergy and Infectious Disease, U.S. Public Health Service, and (in part) by a grant from the National Science Foundation, GB-25986, to the Museum of Zoology, The University of Michigan, for research in systematic and evolutionary biology.

endocones, the splitting of endocones, occurrence of denticles, appearance of a corrugated lateral edge on the hook-body, and tooth deformity.

The mesocones of lateral teeth were consistently straight-sided in population I, angular-sided in population II and intermediate in form in populations III and IV, with one side straight and the other angulated. The endocone of the lateral teeth split differently in the 4 populations. Tooth deformities were observed in the 3 polyploid populations only; these were: lack of one or both cusps in the rachidians, lack of endocones in lateral teeth, and the fusion of 2-3 lateral teeth in populations II, III and IV, respectively.

Statistical analyses demonstrated positive correlations between shell length (age) and (1) number of lateral teeth and (2) number of rachidian teeth in the median longitudinal row. This variation with age reduces the value of radular formulae in taxonomy. The mean tooth width for each size group showed that populations II and IV always had higher values than those of populations I and III.

No differences were found in the general morphology of the nervous system of the 4 populations.

There were no differences in the reproductive system of the 4 populations except: (1) size difference at maturity (hexa- and octoploids being larger), (2) an aphallic condition coupled with lack of uterine pouches in population II, and (3) cordate or pear-shaped preputia in population IV in specimens with shells longer than 6 mm.

The following proportional growth changes were noted: in the young snail the ovotestis is the largest organ and the other reproductive structures are relatively undeveloped; then the male prostate gland reaches full size, and last to mature are the female albumen gland and spermatheca. This order of maturation indicates that bulinines are protandrous hermaphrodites.

Crosses between diploid albino and pigmented snails either revealed mutual cross-fertilization or one-way fertilization (from pigmented to albino). Gene exchange decreased as geographical separation increased.

In crosses between diploid albino and polyploid pigmented snails, when successful, fertilization proceeded in one direction only (from albino to pigmented snails). The offspring were vigorous but sterile. Histologically, sterility was coupled with lack of sperm and an extremely low number of ova. The degree of gene exchange was high in diploid-hexaploid crosses (4/4 experiments) and lacking in diploid-tetraploid (Egyptian) crosses, low in diploid-tetraploid (Ethiopian) crosses and low in diploid-octoploid crosses (0/4, 1/3 and 1/4 experiments respectively being positive). Subsequent back-crossing of hybrid snails to albinos produced egg masses, though embryo mortality was nearly 100%.

F_2 progeny from diploid *Bulinus* crosses, using lack of eye pigment and shell color and shape as genetic markers, demonstrated that lack of eye pigment is inherited as a simple Mendelian recessive character, while shell color and shape characters are presumably polygenic in nature.

Although protandrous hermaphrodites, bulinine snails reproduce, as a rule, by cross-fertilization. Self-fertilization occurs with the depletion of allosperm after isolation. The period of cross-fertilization varied from 2 to 9 weeks after isolation, with a 2-3 week transitory period before self-fertilization was evident, depending on the quantity of allosperm received during copulation.

The electrophoretically separated foot muscle esterases for F_1 hybrids were combinations of the 2 parental patterns.

There were no significant internal anatomical differences among the 4 populations representing the 4 different chromosome numbers in

the polyploid series; shell characters, radulae and pigmentation of the animals showed some insignificant differences. It is, therefore, very difficult to define taxa on the basis of morphological characters and the finer distinctions within groups of *Bulinus* should rely more on cytological and biochemical data in the future. The similarities between populations I and III, and between populations II and IV would seem to reflect their closer relationships. It is suggested that *B. hexaploidus* (population III, n=54) be placed in the *tropicus* group, and *B. octoploidus* (population IV, n=72) the *truncatus* group.

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INTRODUCTION

Snails of the genus *Bulinus* are basommatophoran gastropods possessing a sinistral shell and a pseudobranch. They inhabit freshwaters on the African continent, the circum-Mediterranean areas and the Middle East and are found on some islands in the western Indian ocean. The genus is of medical importance because some of its members are the intermediate hosts of the human trematode parasite *Schistosoma haematobium*. As a consequence, these snails have been studied by a number of investigators. The "subgenus" *Bulinus* (i.e., the *tropicus* group and the *truncatus* group) is further of interest because it contains a series of polyploid species.

Traditionally, the snails which form the subject of this study have been placed in the "subgenus" *Bulinus*. But, because of a nomenclatorial impasse that would have necessitated changes in the well known subgeneric names, including *Bulinus*, Mandahl-Barth (1957) introduced a classification dividing the genus into species groups (1958, 1960, 1965), partly coinciding with the former subgenera. *Bulinus* s.s., the group we are concerned with, was subdivided into 2 closely related species groups in an attempt to distinguish the northern snails, generally susceptible to *Schistosoma*, from the southern generally refractive ones.

In view of the general variability of characters, clear-cut morphological distinction of species is extremely difficult. In recent decades it was sought to supplement the old diagnoses of regional forms, which were largely based on shell characters, with features of internal anatomy. The most significant of the resulting publications are those of Larambergue (1939), Hubendick (1948a, 1948b, 1955), Wright (1956, 1957), Mandahl-Barth (1957, 1958), Demian (1960), Stiglingh, *et al.* (1962), Walter (1968) and van Aardt & van Eeden (1969). However, most of these works present merely uncorrelated anatomical detail. Little attention was paid to variation related to age and season or to genetic or ecophenetically determined characters. Therefore, much of the published data have little practical comparative value, and malacologists are far from agreement on the systematic position and nomenclatorial status of many of the bulinine taxa.

The 2 species groups (*tropicus* and *truncatus*) within *Bulinus* s.s. have been defined by radular characters, the proportions or absence of the male copulatory organ, pigmentation of the animals (Mandahl-Barth, 1957, 1958), by parasitological susceptibility (reviewed by Gismann, 1954; WHO, 1956; Abdel Azim & Gismann, 1956; Dawood & Gismann, 1956; Cridland, 1957; Mandahl-Barth, 1957, 1958; Lo, 1968), to a certain extent by shell characters (Mandahl-Barth, 1965; Schutte, 1965, 1966; Brown, *et al.*, 1967) and, on a finer level, by electrophoresis (Wright, 1965, 1971), cytology (Burch, 1964, 1967a) and immunology (Burch & Lindsay, 1970).

In spite of extremely close morphological similarities in the *tropicus-truncatus* groups, *B. tropicus* and *B. truncatus* show a striking difference in chromosome numbers: *B. tropicus* has the chromosome number (n=18, 2n=36) normal for its family, the Planorbidae (Burch, 1967a, 1967b), whereas *B. truncatus* has exactly twice that number of chromosomes (n=36, 2n=72), indicating tetraploidy (Burch, 1960, 1964). These chromosome numbers appear to coincide with the known parasitological separation of the *Bulinus* s.s. species (Burch & Lindsay, 1970). Also within *Bulinus* s.s. there occur 2 other polyploid forms, *B. hexaploidus* (n=54, 2n=108) and *B. octoploidus* (n=72, 2n=144) (Burch, 1967a, 1972). There are no morphological data (other than shell characters) on either of these polyploid forms, nor any parasitological data on the n=54 form. One n=72 population was found naturally infected in Aden; and Lo (1968) succeeded in infecting another with *Schistosoma haematobium*. The present study was designed to determine if any morphological distinction can be made between members of the polyploid series and to examine how the differences found correlate with the known cytological and parasitological data. Special emphasis was directed to possible growth changes of shell, radula and reproductive system.

In the last decade biochemical and immunological information on bulinine snails has been obtained. Electrophoretic studies of proteins dealt with foot protein (Pace & Lindsay, 1965), egg protein (Wright & Ross, 1965, 1966; Wright, 1971), enzymes (Wright, et al., 1966; Burch & Lindsay, 1967; Wright & File, 1968; Coles, 1969a, 1969b, 1970), blood (Wright & Ross, 1959; Targett, 1963) and whole animal extracts (Rosé, *et al.*, 1966). Immunology was investigated by Burch (1968), Burch & Lindsay (1969, 1970, 1971) and Wright (1971). However, there are, as yet, no cross-breeding or genetic studies which would provide critical information for assessing the taxonomic value of morphological characters and for determining the validity of the lower taxa. The information contained in the current study in regard to cross-breeding contributes to the understanding of interbreeding and isolating mechanisms in nature between members of the "subgenus."

In Africa, the *tropicus* group is widely distributed south of the Sahara, but also off the mainland on Madagascar, while the *truncatus* group is distributed in the northern Mediterranean countries, reaching southward to the great lakes in the east. The *truncatus* group has also been reported from west Africa (Mandahl-Barth, 1958, 1965; Brown & Burch, 1967).

MATERIALS AND METHODS

1. Snails Studied

For comparative studies of shell, pigmentation of animals, radula, nervous system, reproductive system and cross-breeding with another species or population, 4 cytologically distinct and geographically separated populations of *Bulinus* were used. These 4 populations, which form a polyploid series, are designated as populations I, II, III and IV. They were laboratory-bred, except for population III, which was field-collected. Their scientific names, haploid chromosome numbers and origins are given in the chart below.

Population	Scientific name	Haploid chromosome number	Origin
I	*Bulinus tropicus*	n=18	DeVilliers cement reservoir, Malelane, Transvaal, South Africa
II	*Bulinus truncatus*	n=36	Iflaka Bilharzia Project area, Behaira Province, Egypt
III	*Bulinus hexaploidus*	n=54	24 km north of Addis Ababa on Debra Markos Rd., Ethiopia
IV	*Bulinus octoploidus*	n=72	4 km south of Sheno, Ethiopia

In the cross-breeding experiments, 4 additional laboratory-bred populations were used:

V	*Bulinus tropicus*	n=18	Onderstepoort, Transvaal, South Africa
VI	*Bulinus natalensis*	n=18	Lake Sibayi, Zululand, Natal, South Africa
VII	*Bulinus tropicus*	n=18	Lake Baharshangi, Ethiopia
VIII	*Bulinus sericinus*[3]	n=36	Toquor River at Mekerka village, Ethiopia

All populations were mated with the albino *B. tropicus* (Population V).

2. Shell Morphology

Shells of both dead and live snails were taken from the laboratory-bred populations, except for population III, which was field-collected. The shell characters studied were: the shape of spire and aperture, the columella, umbilicus, profiles of outer and inner margins of aperture and body whorl, and the microsculpture of the embryonic and postembryonic whorls. The terminology used for shell parts is shown in Figs. 1-3.

The shell was orientated in such a way that the columellar axis was parallel to the substrate and the outer lip was seen with a minimum of the outer surface of the whorl in view (Fig. 1). Three lines at right angles to the columellar axis, one at the apex, one through the point of attachment of the upper lip to the whorl, and one at the base of the aperture (Fig. 1) demarcate the shell length (L) and aperture length (AL). Two lines parallel to the columellar axis and tangential to the outer lip of the aperture and the body whorl demarcate the aperture width (AW) and shell width (W).

Shells were sorted into size groups termed the 3 mm group, the 4 mm group, etc. (e.g., the 3 mm size group contained individuals of 3.1 - 4 mm shell length). Shells were selected from each of the size groups so as to have a similar size composition for each of the 4 populations (see Fig. 4). Measurements of L, W, AL and AW were made on each shell with an ocular micrometer in a binocular dissecting microscope. The ratios of L/AL, L/W and AL/AW were calculated directly from the data obtained from the micrometer, while L and W were transposed into mm units to the nearest 0.1 mm. Means and standard deviations for each size group and grand means and standard deviations were calculated for L/AL, L/W, AL/AW and W for all 4 populations.

3. Pigmentation of animals

Snails were relaxed with menthol crystals in distilled water for 6-7 hours. The completely relaxed snails were later immersed in hot tap water (approximately 70-80°C) for 1 minute, then fixed and preserved in 30% ethanol. The shells were removed immediately either by twisting them off or by crushing them. Care was taken to minimize injury to the animal, especially when the shell had to be crushed. Photographs were taken (Figs. 13-16) to show mantle markings and pigmentation of the tunica propria, the thin membrane overlying the visceral hump. In all cases, photographs were taken of the animal's left, dorsal and right sides.

4. Radulae

Preserved or dead snails destined for radular study were stored in 70% ethanol.

The buccal mass was extracted from the snail and immersed in 5% potassium hydroxide for a period of 8-48 hours. The cleansed radulae (Figs. 17-18) were stained in 10% chromic acid, usually for 50-60 minutes, but never more than 90 minutes. The stained radulae were placed on a slide and rinsed with a drop of 30% ethanol to remove excess chromic acid. The radulae were spread and flattened on the slide by using 2 camel-hair brushes. After being flattened, absolute ethanol was added to harden and dehydrate the radulae. At this stage each radula could be easily orientated on the slide with the dorsal side up and the posterior end directed anteriorly. The radula was then mounted in Euparal, which was stained green to facilitate microscopic observation.

Two other staining methods were also tried: acetic orcein which stained the bases of the teeth well (Figs. 34-35) and a modification of the oxidation-dahlia technique (Wu, 1965) which offered clear outlines of the hook-bodies of the teeth. Each of the 352 radulae prepared was studied. Figures (Figs. 19-37) were drawn with the aid of a camera lucida.

The shells of animals from which radulae were taken were sorted into size groups as described in Section 2, above. The number of radular preparations used in the statistical analysis were 57, 59, 23 and 50 for populations I to IV respectively (Table 1). The following 6 sets of data were obtained: (1) shell length (L), (2) number of lateral teeth in half a transverse row, (3) number of rachidian teeth in the median

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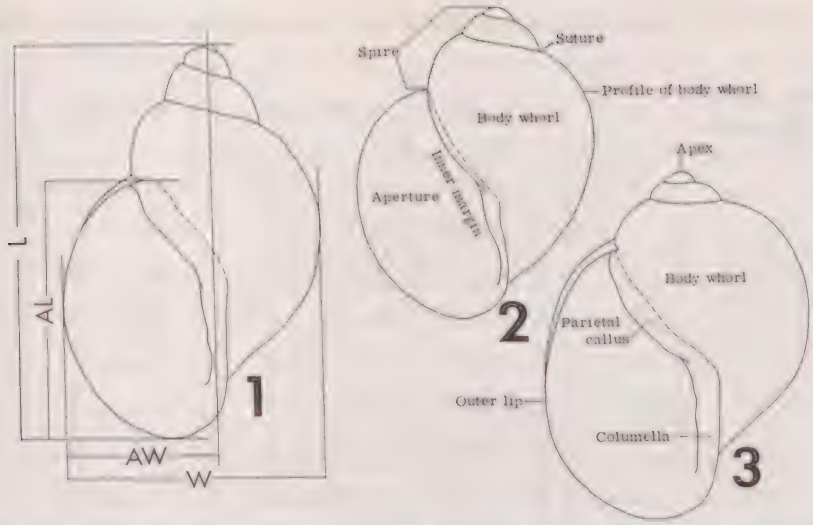
[3]This population was collected by Dr. J. B. Burch on 9 June 1969 (Burch, 1969) from the type locality of *Isidora sericina* and *I. schackoi* Jickeli, 1874. This taxon has been studied by Wright & Brown (1962) and Brown (1965). They concluded that 2 species were originally described from extreme variants of a single population. The L/AL (shell length/aperture length, see Fig. 1) value of *I. sericina* and *I. schackoi* calculated directly from the original data of Jickeli are 1.39 and 1.60 respectively. Since the L/AL value of this population ranged between 1.32 to 1.56, the name *B. sericinus* is used in this report.



FIGS. 1-3. Shells of *Bulinus* (apertural view), showing terminology and measurements used. 1, *B. tropicus*, high-spired, L/AL > 1.51; 2, Albino strain of *B. tropicus*, medium spired, L/AL = 1.31-1.50; 3, *B. natalensis*, low-spired, L/AL < 1.30.

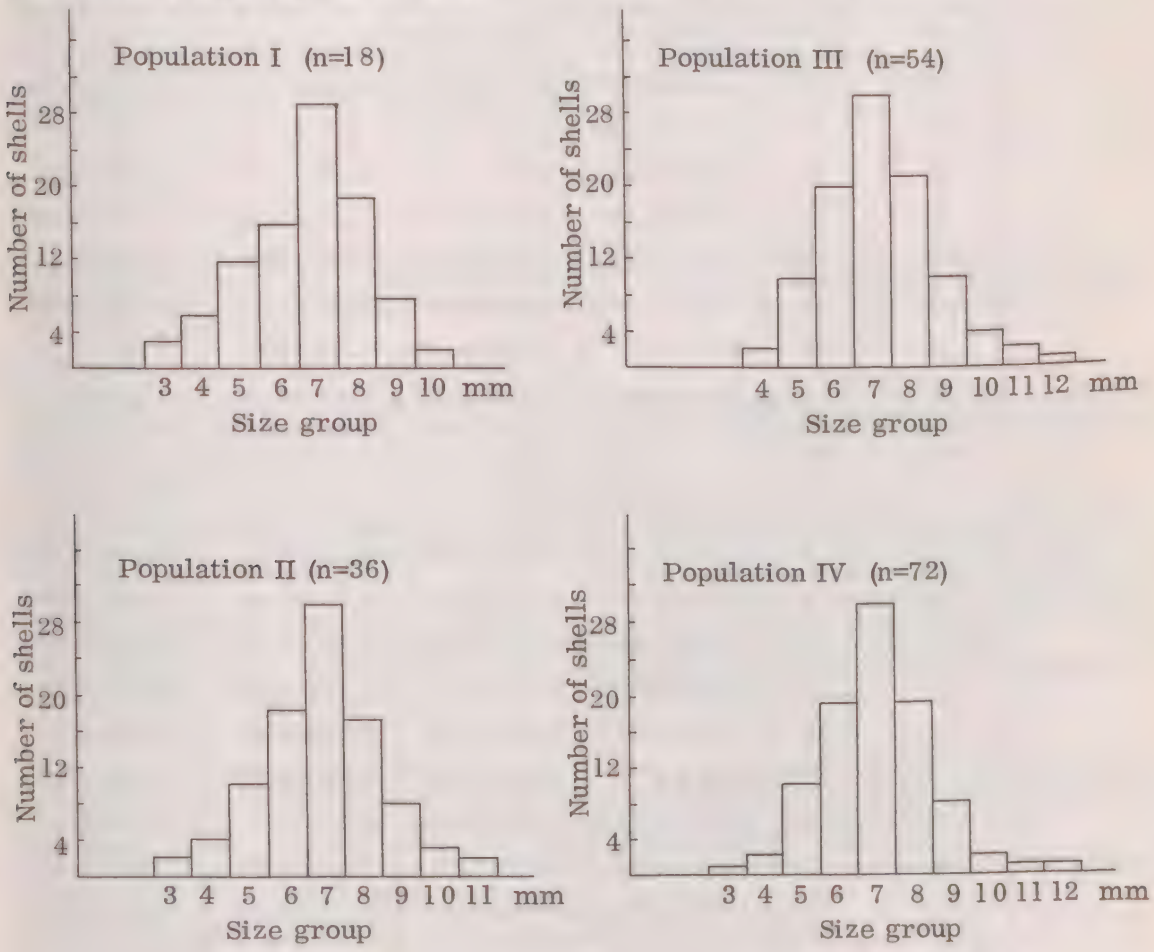


FIG. 4. Size frequency histograms for shells of 4 populations of a polyploid series of *Bulinus*.

TABLE 1. Shell measurements of the 4 populations of *Bulinus* used.

Population	Size group (in mm)	n	L/AL ± SD	L/W ± SD	W ± SD	AL/AW ± SD
I	3	3	1.51 ± 0.04	1.48 ± 0.09	2.60 ± 0.00	1.67 ± 0.05
	4	6	1.44 ± 0.03	1.43 ± 0.07	3.39 ± 0.12	1.75 ± 0.07
	5	12	1.52 ± 0.07	1.50 ± 0.07	3.68 ± 0.26	1.79 ± 0.09
	6	16	1.55 ± 0.11	1.51 ± 0.09	4.36 ± 0.32	1.79 ± 0.11
	7	29	1.53 ± 0.08	1.52 ± 0.07	5.02 ± 0.30	1.80 ± 0.10
	8	19	1.56 ± 0.10	1.50 ± 0.06	5.64 ± 0.23	1.75 ± 0.12
	9	8	1.58 ± 0.06	1.59 ± 0.05	5.84 ± 0.64	1.75 ± 0.03
	10	2	1.65 ± 0.12	1.69 ± 0.11	6.05 ± 0.35	1.93 ± 0.11
	Total n	95				
	M ± SD		1.54 ± 0.09	1.51 ± 0.08	4.77 ± 0.92	1.82 ± 0.11
II	3	2	1.36 ± 0.11	1.35 ± 0.00	2.60 ± 0.00	1.63 ± 0.18
	4	4	1.43 ± 0.10	1.47 ± 0.05	3.33 ± 0.13	1.85 ± 0.09
	5	10	1.52 ± 0.43	1.42 ± 0.05	3.92 ± 0.21	1.67 ± 0.13
	6	18	1.50 ± 0.11	1.43 ± 0.10	4.60 ± 0.37	1.69 ± 0.23
	7	30	1.53 ± 0.07	1.45 ± 0.09	5.24 ± 0.30	1.68 ± 0.09
	8	17	1.55 ± 0.09	1.43 ± 0.10	5.99 ± 0.48	1.62 ± 0.16
	9	8	1.55 ± 0.07	1.48 ± 0.06	6.38 ± 0.30	1.69 ± 0.10
	10	3	1.68 ± 0.08	1.52 ± 0.04	6.83 ± 0.17	1.68 ± 0.10
	11	2	1.54 ± 0.09	1.46 ± 0.05	7.90 ± 0.30	1.66 ± 0.02
	Total n	100				
	M ± SD		1.53 ± 0.17	1.44 ± 0.09	5.18 ± 1.06	1.68 ± 0.15
III	4	2	1.38 ± 0.07	1.62 ± 0.03	2.85 ± 0.05	2.00 ± 0.09
	5	10	1.37 ± 0.03	1.59 ± 0.09	2.05 ± 0.23	2.05 ± 0.09
	6	20	1.37 ± 0.08	1.49 ± 0.12	4.39 ± 0.38	1.94 ± 0.14
	7	30	1.42 ± 0.08	1.57 ± 0.10	4.83 ± 0.35	1.99 ± 0.11
	8	21	1.44 ± 0.10	1.62 ± 0.09	5.42 ± 0.30	2.01 ± 0.11
	9	10	1.42 ± 0.06	1.60 ± 0.09	5.98 ± 0.36	2.02 ± 0.10
	10	4	1.54 ± 0.09	1.67 ± 0.06	6.33 ± 0.18	2.00 ± 0.14
	11	2	1.53 ± 0.00	1.61 ± 0.01	7.10 ± 0.10	1.96 ± 0.04
	12	1	1.41 ± 0.00	1.63 ± 0.00	7.80 ± 0.00	2.11 ± 0.00
	Total n	100				
	M ± SD		1.42 ± 0.09	1.58 ± 0.11	4.95 ± 0.93	1.99 ± 0.12

Table 1 (cont.)

Population	Size group (in mm)	n	L/AL ± SD	L/W ± SD	W ± SD	AL/AW ± SD
IV	3	1	1.35 ± 0.00	1.35 ± 0.00	5.29 ± 0.00	1.67 ± 0.00
	4	2	1.32 ± 0.06	1.31 ± 0.08	3.55 ± 0.05	1.72 ± 0.03
	5	10	1.31 ± 0.05	1.39 ± 0.05	3.99 ± 0.27	1.81 ± 0.08
	6	19	1.38 ± 0.11	1.36 ± 0.08	4.77 ± 0.39	1.73 ± 0.12
	7	30	1.41 ± 0.10	1.38 ± 0.12	5.60 ± 0.31	1.72 ± 0.14
	8	19	1.36 ± 0.06	1.37 ± 0.06	6.22 ± 0.25	1.77 ± 0.11
	9	8	1.43 ± 0.07	1.42 ± 0.07	6.66 ± 0.34	1.71 ± 0.09
	10	2	1.43 ± 0.01	1.39 ± 0.01	7.65 ± 0.15	1.71 ± 0.05
	11	1	1.46 ± 0.00	1.64 ± 0.00	7.00 ± 0.00	1.73 ± 0.00
	12	1	1.51 ± 0.00	1.57 ± 0.00	8.00 ± 0.00	1.74 ± 0.00
	Total n	93				
		M ± SD	1.39 ± 0.09	1.38 ± 0.10	5.48 ± 1.03	1.74 ± 0.12

n, number examined; M, mean; SD, standard deviation; L, Shell length; W, shell width; AL, aperture length; AW, aperture width.

longitudinal row, (4) width of the posterior side of the rachidian tooth (Fig. 28, A), (5) width of the rachidian hook-body (Fig. 28, B), and (6) width of the hook-body of the 1st lateral tooth (Fig. 28, C). The measurements of the 3 latter sets of data were made with an ocular micrometer. Means and correlation coefficients were also calculated.

5. Nervous system

Preserved specimens (treated as described in Section 3) were mostly used for dissection and study of the nervous system. Bouin's solution often gave good results with fresh or refixed specimens. Figs. 47-49 were drawn using a Wild microscope and a camera lucida.

6. Reproductive system

Preserved specimens (as in Section 3) were used. The entire reproductive system was dissected out and drawn with the aid of a camera lucida. Animals with shell sizes of approximately 3, 4.5, 6, 7.5 and 9 mm length, representing ages of 12, 22, 32, 48 and 60+ days, respectively, after hatching (see growth curve, fig. 2 of Lo, 1968) were especially described. Estimation of surface ratios of albumen gland/prostate, spermatheca/prostate and ovotestis/albumen gland for each size group as those of Section 2 was made from camera lucida drawings, the surface being that area shown in the drawing.

For comparison of ovotestes between normal snails and sterile hybrids, and for the detailed structure of the carrefour complex, serial sections were stained with hematoxylin-eosin.

7. Cross-breeding experiments

The albino strain of laboratory-bred *Bulinus tropicus* from Onderstepoort, Transvaal, South Africa, was cross-bred with the other 7 pigmented populations. The albino snail had the haploid chromosome number 18 and lacked both eye and body pigmentation. In general, only the eye-pigmentation character was used as a genetic marker, but in experiment 2 shell color and shape was also used.

The following cross-breeding experiments were carried out between the albino *Bulinus tropicus* (population V, n=18) and pigmented *Bulinus* populations:

1. Albino x *B. tropicus* (pop. I, n=18) Crosses A, B.
2. Albino x *B. natalensis* (pop. VI, n=18) Crosses C, D, E.
3. Albino x *B. tropicus* (pop. VII, n=18) Crosses F, G, H, I.
4. Albino x *B. truncatus* (pop. II, n=36) Crosses J, K, L, M.
5. Albino x *B. sericinus* (pop. VIII, n=36) Crosses N, O, P.
6. Albino x *B. hexaploidus* (pop. III, n=54) Crosses Q, R, S, T.
7. Albino x *B. octoploidus* (pop. IV, n=72) Crosses U, V, W, X.

The snails (2 in inter-populational and test crosses, and 5-7 in brother-sister breeding of F_1) were cultured in 15 cm petri-dishes having mud in their centers and containing approximately 65 cc of spring water or aged tap water. A piece of lettuce softened by dipping in boiled water for 1-2 seconds was supplied to each dish. The size of the lettuce provided varied depending on the number and size of snails. An area of approximately 1 cm^2 is consumed by an average size snail (6-7 mm in shell length) within 2 days. The water was replaced on alternate days. The cultures were kept at room temperature (21-29°C).

Only young snails less than 3 mm in length were used to assure that the snails were virgin, since snails of that size are not reproductively mature. One snail each from the 2 populations to be crossed were put together in a dish until the 1st egg mass was laid. The "parents" were then separated, each being thereafter placed in a new dish at 1-week intervals to separate them from their egg masses or hatching offspring. Eye pigment of progeny was checked and recorded prior to the hatching of the young snails.

For the sibling mating of the F_1 progeny, the young snails were reared in groups not exceeding 7, so as to assure normal growth. They were kept together until they had mated and spawned, i.e., for a week after observing the 1st egg mass. The presence or absence of eye-pigment in F_2 progeny was recorded prior to hatching.

In back-crosses, the F_1 progeny from either pigmented or albino parents were back-crossed to an albino. The methods of observation and recording were the same as those described above. Eventual back-crossed progeny were followed for only 6 weeks after the spawning of the 1st egg mass. In the cross-breeding experimental series 4 and 5, all the F_1 progeny of about 4 mm length were temporarily anesthetized and euphallic snails were selected. After recovering from relaxation these were back-crossed to an albino. In this way, the possibility of reciprocal mating was assured.

8. Electrophoresis

Polyacrylamide gel disc electrophoresis was used to obtain further evidence of cross-fertilization between the albino and pigmented snails. Foot muscle esterase patterns of adult F_1 and parent snails were compared. The esterases were obtained from pooled tissues. The technique applied was that recommended and described in detail by Davis & Lindsay (1967). The diagrams (Figs. 102-106 B) of foot muscle esterase fractions were obtained from (1) direct visual inspection of the stained gels, and (2) densitometric tracings of the stained gels (Figs. 102-106 C) with a Photovolt Densicord Densitometer (Model 552). For comparison between runs that did not measure exactly the same length, calculations were made of mean R_f[4] values and standard deviations of each fraction observed for adult F_1 and parental snails (Crosses A, E, O, R and V).

RESULTS

I. Shell Morphology

1. General Description of the Shell of *Bulinus* "s.s."

The shell (Figs. 1-3, 5-8) is sinistral. Its shape is globose, oval or ovate. The spire of the shell is high (Fig. 1), medium (Fig. 2) or low (Fig. 3); its apex can be sharply pointed (Figs. 1, 5, 6) or blunt (Fig. 8). The suture is pronounced. The profile of the body whorl is evenly rounded. The aperture (Figs. 1-3) is round, oval, ovate or lanceolate. The outer lip of the aperture is sharply edged or evenly rounded. The upper half of the inner margin is formed by the parietal callus, the lower half by the columella (Fig. 3). The parietal callus may be clearly defined or indeterminate and the columellar edge may be sharp or expanded and reflexed. The upper portion of the columellar edge may be adnate to the body whorl, concealing the umbilicus. The umbilicus is occasionally "open" in snails longer than 9 mm. The middle portion of the inner margin is either straight (Fig. 6) or shows a more or less marked concavity (Figs. 1-3, 8). The embryonic shell has microscopic, regularly arranged punctae (Walter, 1962, 1968) and the 1st whorl of the postembryonic shell always has regularly spaced ribs. The ribs gradually decrease in prominence from the 2nd whorl on. Consequently, the surface of the body whorl may show a trace of ribbing or may be smooth. In some shells prominent ribs also persist on the body whorl (see Figs. 12-13, Burch, 1967b).

The shell color varies from almost pure white to dark brown, but usually is light or dark brown. Field-collected specimens (population III) were coated with a black deposit.

2. Comparison of Species

Population I (*Bulinus tropicus*, n=18). Figs. 5, a-g

The spire is high, the mean of the ratio L/LA being 1.54 (Table 1) and the range 1.36-1.82. Its shape is conical or sharply pointed toward the apex. The outlines of the body whorl and outer lip of the aperture are rounded, the inner margin of the aperture is slightly concave in its middle portion. The shell microsculpture of the embryonic and apical whorls is as described above; the body whorl has regularly spaced low ribs; the surface between the ribs is not smooth. The shell is dark brown.

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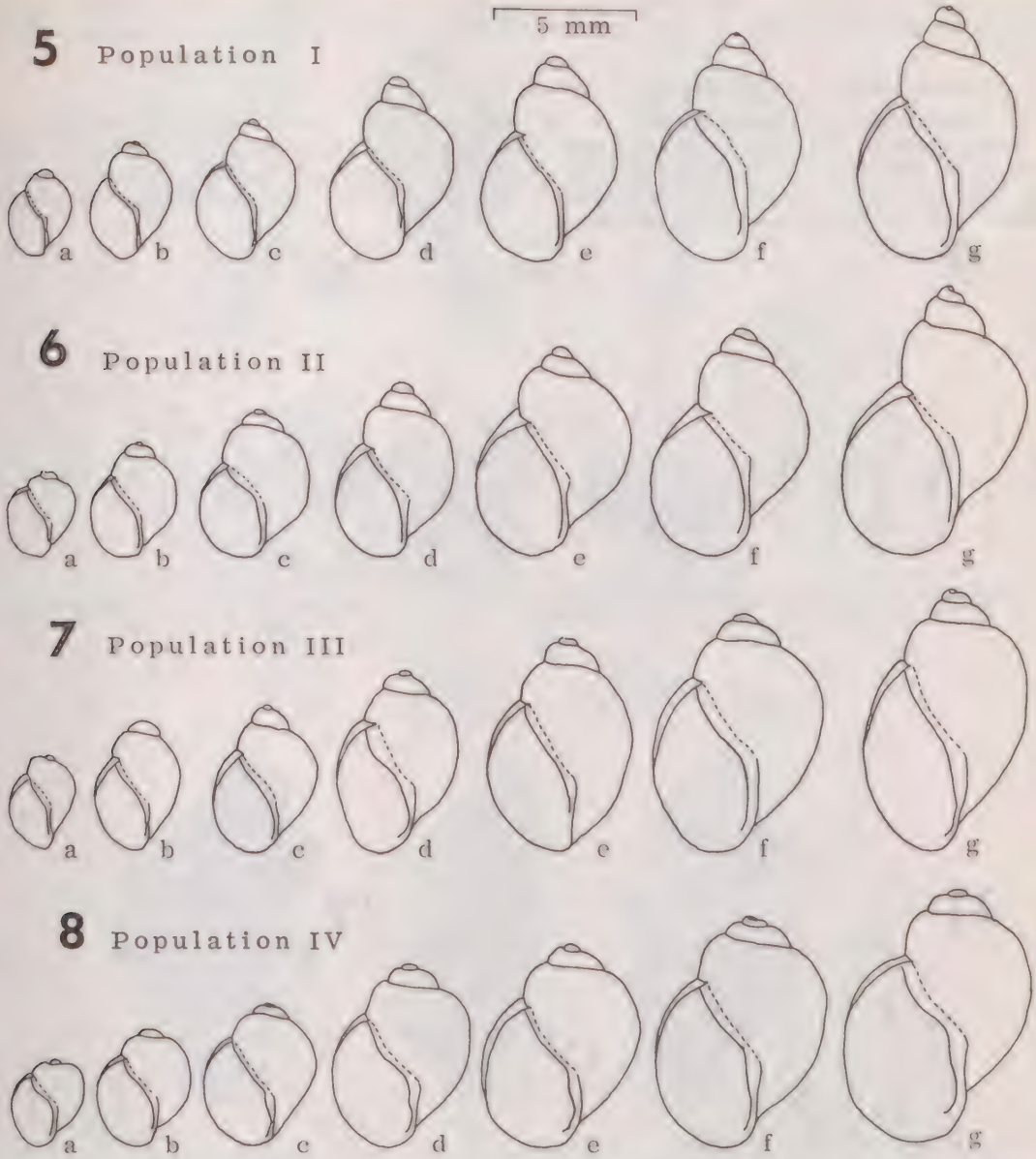
[4] R_f is the ratio of the distance from the origin to each band and to the front of the separation.



FIGS. 5-8. Shells of 4 populations of bulinine snails in aperture view, size groups a-g represent sizes from 3-9 mm. 5, Population I, *Bulinus tropicus*, n=18; 6, Population II, *B. truncatus*, n=36; 7, Population III, *B. hexaploidus*, n=54; 8, Population IV, *B. octoploidus*, n=72.

Population II (*Bulinus truncatus*, n=36). Figs. 6, a-g

The spire is high, the mean of L/AL being 1.53 (Table 1) and the range 1.25-1.79. It has a pointed apex. The contours of the body whorl and the outer lip of the aperture are more flatly rounded than in the *Bulinus tropicus* population. The inner margin of the aperture is nearly straight. The aperture is more round than that of *B. tropicus*. Shells longer than 9 mm may have an open umbilicus, probably due to erosion of the reflected columellar edge where it is adnate to the body whorl. The shell microsculpture is slightly more prominent than that in *B. tropicus*; the surface between the ribs is smooth. The shell is whitish or light brown.

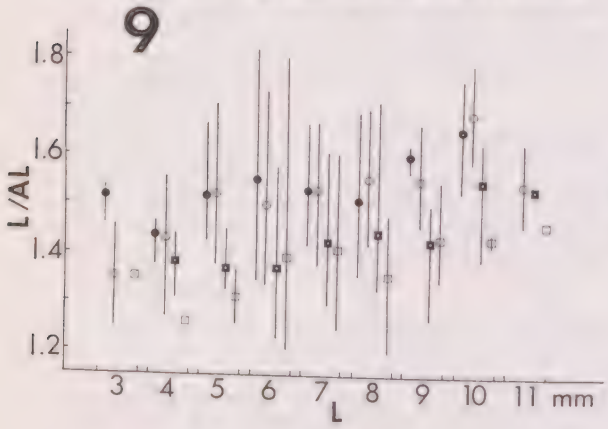
Population III (*Bulinus hexaploidus*, n=54). Figs. 7, a-g

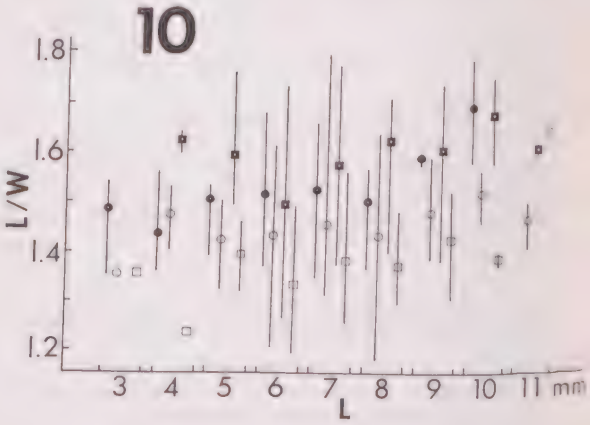
The spire is of medium height, the mean of L/AL being 1.41 (Table 1) and the range 1.23-1.71. It has a less pointed apex than the above 2 species. The contours of the body whorl and the outer lip of the aperture are rounded and similar to those of *Bulinus tropicus*. The inner margin of the aperture is slightly

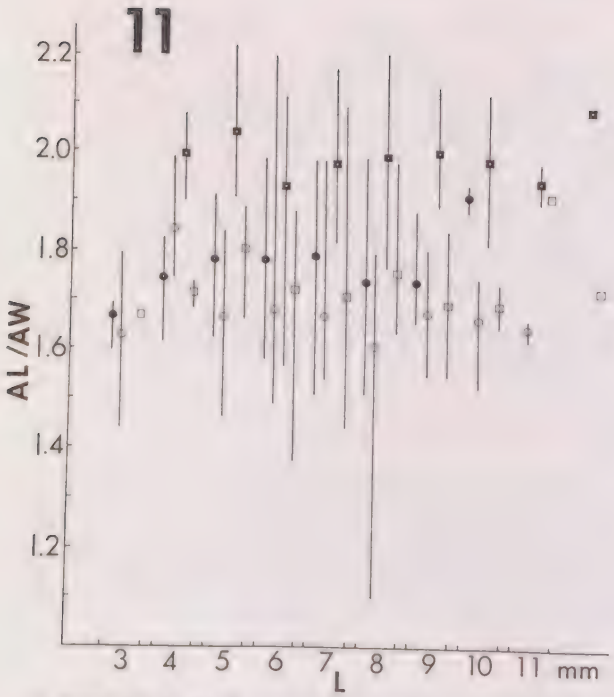
concave in its middle portion. The aperture is elongate-ovate, the mean of AL/AW being higher than in the other populations (1.99, Table 1). The shell microsculpture is like that of *Bulinus truncatus*. The color is dark brown.

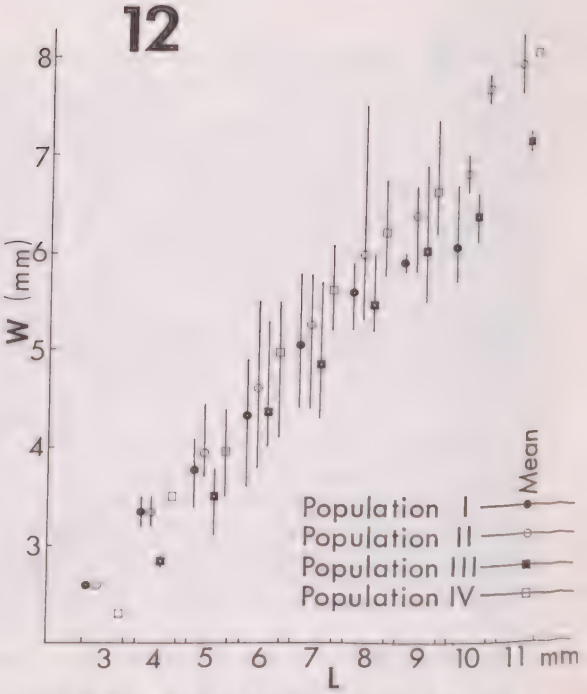
Population IV (*Bulinus octoploidus*, n=72). Figs. 8, a-g

The spire is of medium height, the mean of L/AL being 1.39 (Table 1) and the range 1.20-1.80. Its apex is bluntly pointed. The aperture is large and ovate, the mean of AL/AW being 1.74 (Table 1). The contours of the body whorl and the outer lip of the aperture are more round than those of *Bulinus truncatus*. The inner margin of the aperture is concave in its middle portion. The shell microsculpture is as in *Bulinus tropicus*. The shell is light to dark brown.









FIGS. 9-12. Shell measurements in the different size groups (shell length, L) for populations I-IV, showing range and mean. 9, The ratios shell length/aperture length (L/AL); 10, The ratios shell length/shell width (L/W); 11, The ratios aperture length/aperture width (AL/AW); 12, Shell width.

FIGS. 13-16. Pigmentation in animals of 4 populations of a polyploid series of *Bulinus* (a, left side view; b, dorsal view; c, right side view). 13, Population I, *Bulinus tropicus*, n=18; 14, Population II, *Bulinus truncatus*, n=36; 15, Population III, *Bulinus hexaploidus*, n=54; 16, Population IV, *Bulinus octoploidus*, n=72.

3. Measurements and Ratios of Shells

Sample numbers, means of width and of 3 ratios (L/AL, L/W, AL/AW) for the 4 populations, as well as their respective standard deviations for each size group, are given in Table 1; sample means for each of the above sets of data are also presented.

The ranges and mean of each set of data above were plotted against the size groups (Figs. 9-12).

II. Pigmentation of Animals

Population I (*Bulinus tropicus*, n=18). Figs. 13, a-c

The head and foot regions are dark. White flecks are uniformly scattered over their surface except at their periphery (anterior margin of snout, the superior tentacle lobe and the edge of the foot where they are usually intensely aggregated). These peripheral margins always appear yellow-green in menthol-relaxed specimens.

The mantle always has distinct black blotches and patches. The patterns are irregular and variable, depending on the individual snail. The tunica propria of the visceral hump is transparent, except for the black area overlying the ovotestis.

Population II (*Bulinus truncatus*, n=36). Figs. 14, a-c

The head and foot regions are lighter in color than those of *Bulinus tropicus* and the peripheral margins of the head and foot regions are not yellow-green. The anterior portion of the head and the posterior region of the foot are relatively darker than the rest.

White flecks are scattered over the head region, 2 white patches of densely aggregated flecks always being present at a position anterior and medial to the eyes (Fig. 17). In general, white flecks are rather densely scattered on the tentacle lobe and tentacles, and sparsely scattered in the foot region.

Neither the mantle nor the tunica propria of the visceral hump are pigmented. The mantle is pale gray without any black spots; only insignificant amounts of black pigment are seen about the edges of the kidney and blood vessels of the mantle.

Population III (*Bulinus hexaploidus*, n=54). Figs. 15, a-c

The color of the head and the foot regions and the distribution of white flecks are as in *Bulinus tropicus*.

The mantle has dark gray to black irregular patches on a grayish background. The tunica propria of the visceral hump is uniformly pigmented, in the same shade of black as that of the mantle markings.

Population IV (*Bulinus octoploidus*, n=72). Figs. 16, a-c

The animal is light in color, as *Bulinus truncatus*. However, the distribution of white flecks is as in *B. tropicus*, except that the white flecks are less densely distributed on the side of the foot.

Neither the mantle nor the tunica propria of the visceral hump are pigmented. Insignificant amounts of black pigment are seen in the areas of the kidney and blood vessels and in the tunica propria that overlies the ovotestis.

III. Radulae

1. Orientation of Bulinine Radulae

Each individual bulinine tooth, whether rachidian, lateral or marginal, is basically a hook which consists of 3 parts: cusp, hook-body and base. These are shown in lateral view for an innermost lateral tooth in Fig. 22. During the spreading and flattening necessary to get the radula properly orientated on a microscope slide, some radular teeth are tilted, and at different angles. Therefore, only transverse rows that had the same orientation as that of their corresponding rachidian teeth were chosen for study. Five main types of orientation (Figs. 20, A-E) of the rachidian teeth were distinguished. Those in which the tips of the cusps are seen to jut out over the posterior end of the rachidian base are here designated as having orientation "A" or "B", the former jutting out further than the latter (Figs. 20A and 20B). In "C" orientation the tip of the cusp is seen to lie over the posterior edge of the rachidian base, (Fig. 20C); in "D" orientation it is slightly anterior to the posterior end of the rachidian base (Fig. 20D), and in the "E" orientation it is far anterior (Fig. 20E).

Under microscopic observation there are 3 main planes of focus: "high," in which the cusps distinctly show (Fig. 23); "medium," in which the hook-body shows distinctly (Fig. 24); and "low," in which the base of the tooth shows distinctly (Fig. 25).

In any individual radula the teeth from anterior, middle and posterior portions show some morphological variation (Figs. 26-28). Teeth located anteriorly (Fig. 26) are functional and thereby worn, while those located posteriorly (Fig. 28) are in the process of being developed and are still unused. Only those located between (Fig. 27) these anterior and posterior positions are fully developed and not yet subjected to significant wear.

For comparative purposes, transverse radular rows of the 4 populations situated at about 30 ± 5 rows back of the anterior rachidian tooth are described and drawn here (Figs. 31-34). All figures have the "D" orientation and represent a composite of the different focus levels.

Because of extreme overlapping, the complete outline of any single tooth is difficult to obtain, especially for the intermediate lateral and outer lateral teeth. This difficulty can be overcome by observing the most

FIG. 17. Head of *Bulinus truncatus*, dorsal view; showing the dense aggregation of white flecks.

anterior teeth in a longitudinal row, which usually have worn cusps while the base and the hook-body portion (Figs. 20, B-D; Figs. 35-38) are distinct.

2. General Morphology

The ribbon-like bulinine radula has a length 2-3 times its width when it is flattened on the slide. In the natural condition, the anterior portion of the radula expands into the posterior portion of the buccal cavity, and the posterior half of the radula forms a cylindrical sac (Figs. 18-19) which lies over the odontophoral cartilage in the middle of the body axis. Each radular ribbon contains many transverse rows of teeth similar to one another, except that in the anterior functional portion the teeth are subjected to wear and tear; moreover, approaching the anterior edge, each transverse row has fewer teeth.

When the radula is flattened on the slide, each transverse row of teeth is slightly arched, the concavity of the curve being directed toward the posterior end. Each transverse row contains a rachidian tooth and many lateral teeth[5] on each side (20-30 as the snail increases in size).

The rachidian has 2 cusps and may or may not have a groove on the hook-body (Fig. 31 with, Fig. 32 without). Sometimes a denticle ("interstitial cusp") occurs between the cusps. The base of the rachidian is trapezoid-shaped, with a broad, concave posterior side and a shorter, straight anterior side (Figs. 20, A-E; 30, A-C). In dorsal view, the anterior side of the base is concealed by the hook-body.

Several innermost lateral teeth are typically tricuspid (Figs. 31-34). The 3 cusps are conventionally called "endocone, mesocone and ectocone" (see Baker, 1928). The endocone is either triangular or expanded and corrugated (Figs. 26-27). The mesocone is the largest and strongest of the 3 cusps. It is triangular in shape or nearly so, either with smoothly curving (Fig. 31) or angular sides (Fig. 32), or "intermediate" i.e., with one side angular while the other is smoothly curved (Figs. 33-34). The ectocone is usually triangular. In some species the lateral edge of the hook-body is corrugated or serrated. Sometimes slender denticles are present between the cusps. Denticles between the mesocone and the endocone always seem to be on the side of the endocone (Figs. 23, 27). The base of each inner lateral tooth is in the shape of a parallelogram (Figs. 25, 29). Although each tooth slightly slants medially, its cusps and hook-body tend to curve directly over their own bases.

The intermediate lateral teeth (Fig. 36) and outer lateral ("marginal") teeth (Fig. 37) are basically tricuspid hooks, though modified. The modifications observed are: (1) the endocone splits into 4-6 equal sized cusps; (2) the mesocone becomes smaller; (3) the ectocone also becomes smaller, and lower in position; (4) the hook-body elongates and slants in a medio-posterior direction; (5) a corrugated or serrated edge distinctly appears on the lateral edge of the hook-body and disappears as the teeth approach the outer margin; and (6) the base is square rather than in the shape of a parallelogram.

The outermost 2 teeth (Fig. 38) are modified as above, but the cusps and base are not clearly defined.

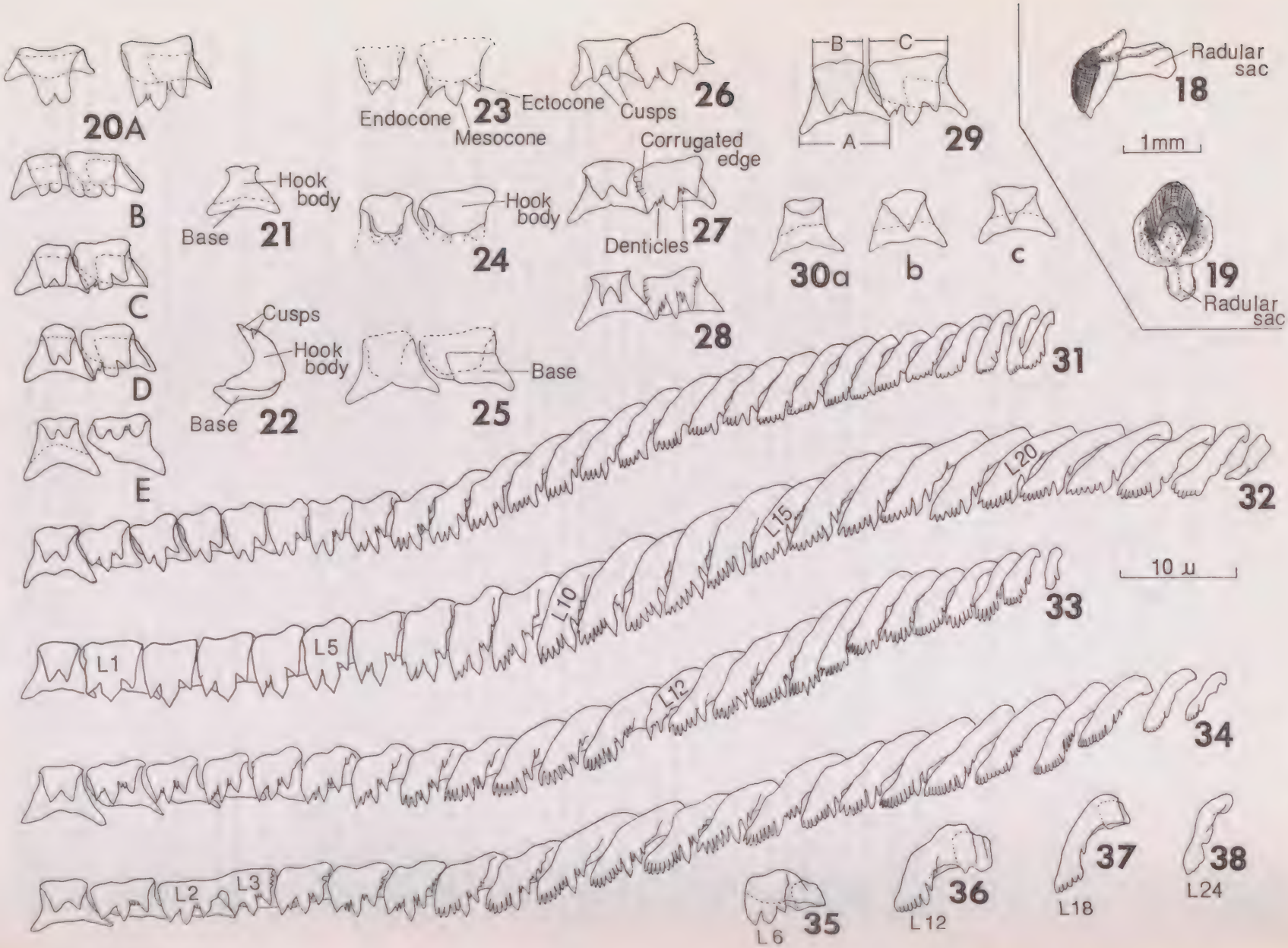
3. Comparison of Species

Population I (*Bulinus tropicus*, n=18). Fig. 31

Rachidian tooth. As described above, with very little modification or variation. There was very little radular variation in the 108 specimens studied.

Lateral teeth. The 1st lateral tooth (L1) has a triangular endocone and a triangular ectocone, both of which are shorter than the prominent, smoothly curved triangular mesocone. A denticle is often present between the mesocone and ectocone. From L4 or L5 onward, the endocone becomes larger than that in L1

[5]The lateral and marginal teeth cannot be morphologically delimited with certainty, because there is a more or less gradual transition between them. Therefore, the marginal teeth throughout this paper will be included with, and referred to, as the lateral teeth. The lateral teeth are numbered L1, L2, L3, etc., in consecutive order, from the middle of the radula toward the margin.


20A
B
C
D
E
Hook body
Base
21
Endocone
23
Ectocone
Mesocone
Cusps
26
Hook body
24
Corrugated edge
Denticles
27
B
C
A
29
28
Cusps
Hook body
Base
22
Base
25
30a
b
c
Radular sac
18
1mm
19
Radular sac
31
32
L20
L15
L10
L5
L1
10 µ
33
L12
34
L2
L3
L6
35
L12
36
L18
37
L24
38

and L2, and attains the same height as the mesocone. The endocones of the lateral teeth split into 2 cusps at L7 or L8, and from L8 or L9 on into 3, 4, 5 and 6 cusps at intervals of every 3 teeth. The corrugated or serrated lateral edge of the hook-body becomes apparent from L7 or L8 on, but, as the teeth approach the outer margin, it becomes a mere bump and disappears.

Population II (*Bulinus truncatus*, n=36). Figs. 30, a-c; Fig. 32

Rachidian tooth. Same as above, generally with little variation. However, 3 types of rachidian deformities are occasionally observed: the lack of a cusp on either the left side or the right side (Figs. 30b, 30c), or a lack of both right and left cusps (Fig. 30a). The frequency of these 3 deformities, on 3 different occasions, in the same population were:

No. of individuals examined	Time of radular preparation	No. of normal rachidians	Number of teeth with missing		
			right cusp	left cusp	both cusps
50	July 1969	20	2	15	13
50	Aug. 1969	43	1	4	2
50	Mar. 1970	49	0	1	0

Lateral teeth. The endocone of L1 is large and has almost the same height as the neighboring mesocone. It is sometimes serrated medially and may have a denticle on the lateral side. The mesocone is large and angular-sided as described by Mandahl-Barth (1957), Brown, *et al.* (1967) and Walter (1968). The ectocone is triangular in shape and is smaller than the endocone and mesocone. A denticle may or may not be present between the endocone and mesocone and between the mesocone and ectocone. The endocones of the lateral teeth split into 2, 3, 4 and 5 cusps in L6 or L7, L8, L9 and L10 respectively. There are 6 cusps at L12 and 7-8 cusps at L16. The corrugated or serrated lateral edge of the hook-body is noticeable from L7 or L8 onwards.

Population III (*Bulinus hexaploidus*, n=54). Fig. 33

Rachidian tooth. Same as above, with little variation. Among 42 specimens examined, 1 specimen lacked the left cusps and 1 specimen had an extremely narrow hook-body.

Lateral teeth. The endocone and ectocone of L1 is the same as that in the *Bulinus tropicus* population described above. The mesocone has one side angular and the other side straight or evenly rounded. There usually are 1-2 denticles between the endocone and mesocone and between the mesocone and ectocone of L1-L4. The endocones of L3 or L4 begin to expand and gradually increase to attain the same height as their mesocones. The endocones of the lateral teeth split respectively into 2, 3, 4, 5 and 6 cusps at L5 to L7, at 1-tooth intervals. The serrated and corrugated edge of the hook-body becomes apparent and strong at L3 or L4.

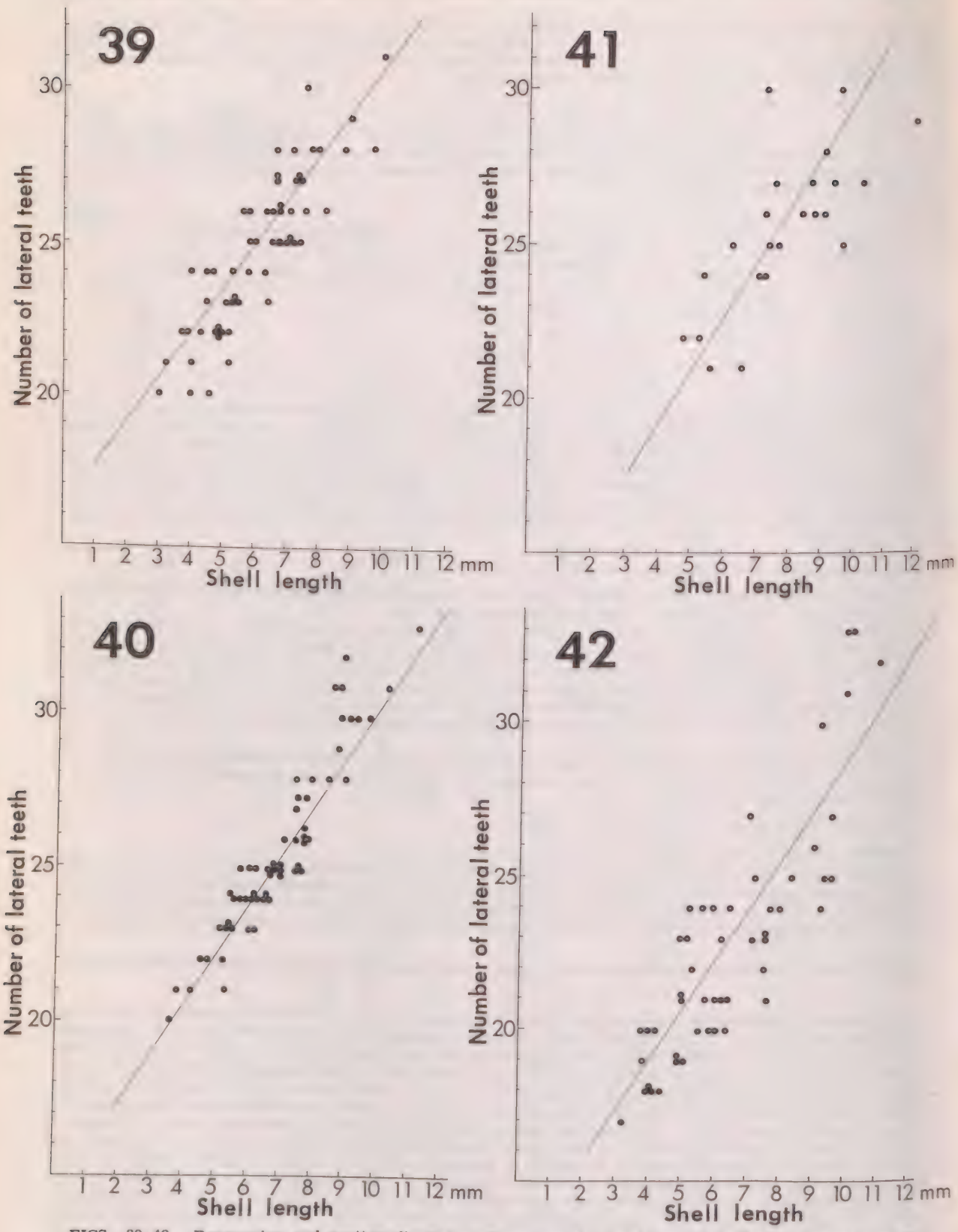
Among the 42 specimens examined, 4 had abnormalities in one complete longitudinal row of teeth and 1 specimen had abnormalities in 2 such rows of teeth. The abnormalities consisted in a missing endo- or ectocone (see Fig. 33, L12).

Population IV (*Bulinus octoploidus*, n=72). Fig. 34

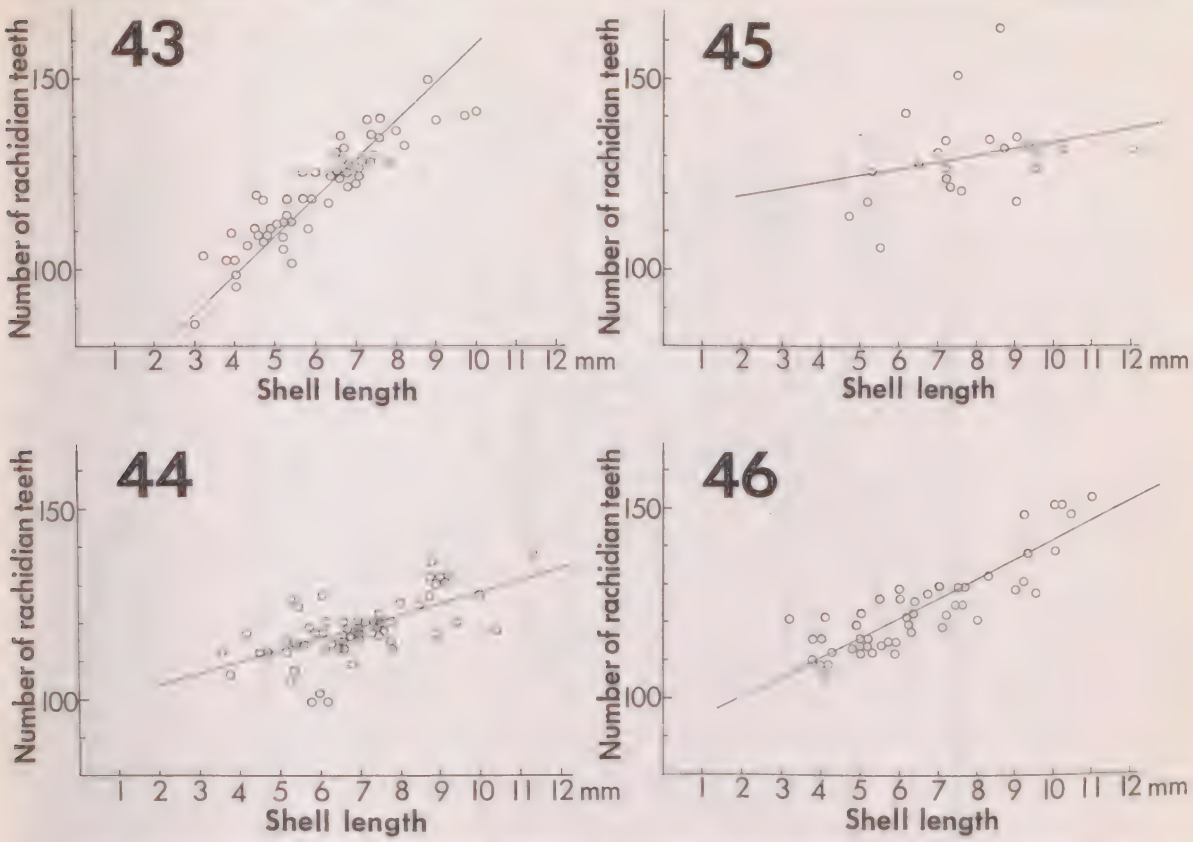
Rachidian tooth. Same as above, with little or no variation.

Lateral teeth. The endocone of L1 is large and expanded. It attains the same length as its mesocone. The mesocone has one side angular and the other side evenly curving. One denticle usually is present on the lateral side of the endocone; 2-3 denticles are nearly always present between the mesocone and ectocone. The corrugated or serrated edge on the lateral edge of the hook-body is evident, beginning with L3.

FIGS. 18-38. Radulae of the 4 bulinine populations compared: 18, The intact radular complex of population I (dorso-lateral view); 19, The intact radular complex of population I (dorsal view); 20, A-E. Rachidian and L2 tooth (A) and rachidian and L1 teeth (B-E) of population III tilted at slightly different angles (dorsal view); 21, Rachidian tooth of population III (anterior view); 22, L6 tooth of population III (lateral view); 23-25, Rachidian and L1 teeth of population III, focused at high, middle and low levels respectively (dorsal view); 26-28, Rachidian and L1 teeth of population III, from anterior, middle and posterior portions of same radula (dorsal view); 29, Rachidian and L1 teeth of population III, showing the width of posterior edge of rachidian base (A), width of hook-body of rachidian (B) and width of hook-body of L1 tooth (C) (dorsal view); 30, Rachidian teeth of population II, showing cusp deformities (a-c) (dorsal view); 31, Half a transverse row (ca. 30±5) of population I at "D" orientation (dorsal view); 32, Half a transverse row (ca. 30±5) of population II at "D" orientation (dorsal view); 33, Half a transverse row (ca. 30±5) of population III at "D" orientation (dorsal view), showing cusp deformity at L12; 34, Half a transverse row (ca. 30±5) of population IV at "D" orientation (dorsal view), showing tooth anomalies (fusion) in L2 and L3; 35-38, The most anteriorly located L6, L12, L18 and L24 of population III(dorsal view).



FIGS. 39–42. Regression and scatter diagrams of number of lateral teeth in half a transverse row on shell length. 39, Population I; 40, Population II; 41, Population III; 42, Population IV.



FIGS. 43-46. Regression and scatter diagram of number of rachidian teeth in median longitudinal row on shell length. 43, Population I; 44, Population II; 45, Population III; 46, Population IV.

The endocones of the lateral teeth split respectively into 2-3, 3-4, 5, 6, 7, 8 and 9 cusps about L5, L6, L7, L8, L9, L10 and L11 respectively.

In the 52 specimens examined, 19 specimens had a fusion of 2-3 teeth among the innermost 5 lateral teeth (see Fig. 34, L2-L3). Ten of them had teeth fused on both sides of the rachidian tooth, either symmetrically or asymmetrically placed, and 9 specimens had tooth fusion on only one side. The fusion of teeth occurred only at the hook-body and not at the base.

4. Statistical Analyses

For the 4 populations, scatter diagrams were plotted showing shell length against number of lateral teeth in half a transverse row (Figs. 39-42) and shell length against number of rachidians in the median longitudinal row (Figs. 43-46). The correlation coefficients (r) calculated for shell length and number of lateral teeth in half a transverse row were 0.855, 0.925, 0.732 and 0.858 for populations I to IV respectively. The values of r for n - 1 degree of freedom (i.e., 56, 58, 22 and 49 for populations I to IV respectively), at p=0.01, are 0.337, 0.331, 0.517 and 0.356 respectively (see table 64, Bishop, 1966). The actual values obtained are significantly larger than the values for the n - 1 degree of freedom. Therefore, there is a positive correlation between shell length and number of lateral teeth. The correlation coefficients calculated for shell length and number of rachidian teeth in the median longitudinal row were 0.897, 0.587, 0.253 and 0.882 for populations I to IV respectively. These values also are significantly larger than those for the n - 1 degree of freedom, except for population III, 0.253, which was smaller than 0.517. Therefore, there is also a positive correlation between shell length and number of rachidian teeth in the median longitudinal row.

The mean widths of the posterior edge of the rachidian base (RP), of the rachidian hook-body (RH) and width of the hook-body of the 1st lateral (LH) in the different size groups are tabulated in Table 2 and presented graphically in Fig. 47. These data indicate that there is a positive correlation between the width of teeth and shell length. Comparison of mean values for RP and LH showed that those for populations II and IV are larger than those of populations I and III from 3 mm shell length up to 7 mm, whereas for RH only those of population IV are larger.

TABLE 2. Mean sizes in μ of the widths measured in various radular teeth in the 4 populations used.

Size group (in mm)	Population I				Population II				Population III				Population IV			
	n	RP	RH	LH	n	RP	RH	LH	n	RP	RH	LH	n	RP	RH	LH
3	6	15.0	7.9	11.2	2	17.5	8.2	12.5	-				5	15.2	9.3	12.2
4	10	16.7	9.6	12.5	3	17.1	8.8	13.7	1	15.0	10.0	12.5	11	17.7	11.1	14.2
5	12	18.9	10.6	14.2	13	20.0	10.6	16.1	3	19.6	10.8	15.8	9	19.7	12.5	16.5
6	12	20.2	11.6	15.2	17	20.7	11.3	17.6	3	20.8	12.5	16.2	6	21.7	12.7	17.5
7	12	20.7	12.4	16.1	12	22.0	12.5	18.1	6	21.6	12.5	17.5	8	23.4	13.9	19.4
8	3	20.4	12.1	15.4	7	22.3	13.0	19.4	5	24.7	13.7	19.7	2	23.8	14.4	20.0
9	2	21.9	12.5	16.3	3	22.5	12.0	19.2	3	25.0	15.0	20.8	6	25.0	14.0	20.8
10	-				1	25.0	12.5	20.0	1	27.5	15.5	21.2	3	25.0	14.2	20.0
11	-				1	25.0	13.7	20.0	1	27.5	15.5	22.5	-			
Total sample	57				59				23				50			

n, numbers measured; RP, mean width of posterior side of rachidian; RH, mean width of hook-body of rachidian; LH, mean width of first lateral tooth.

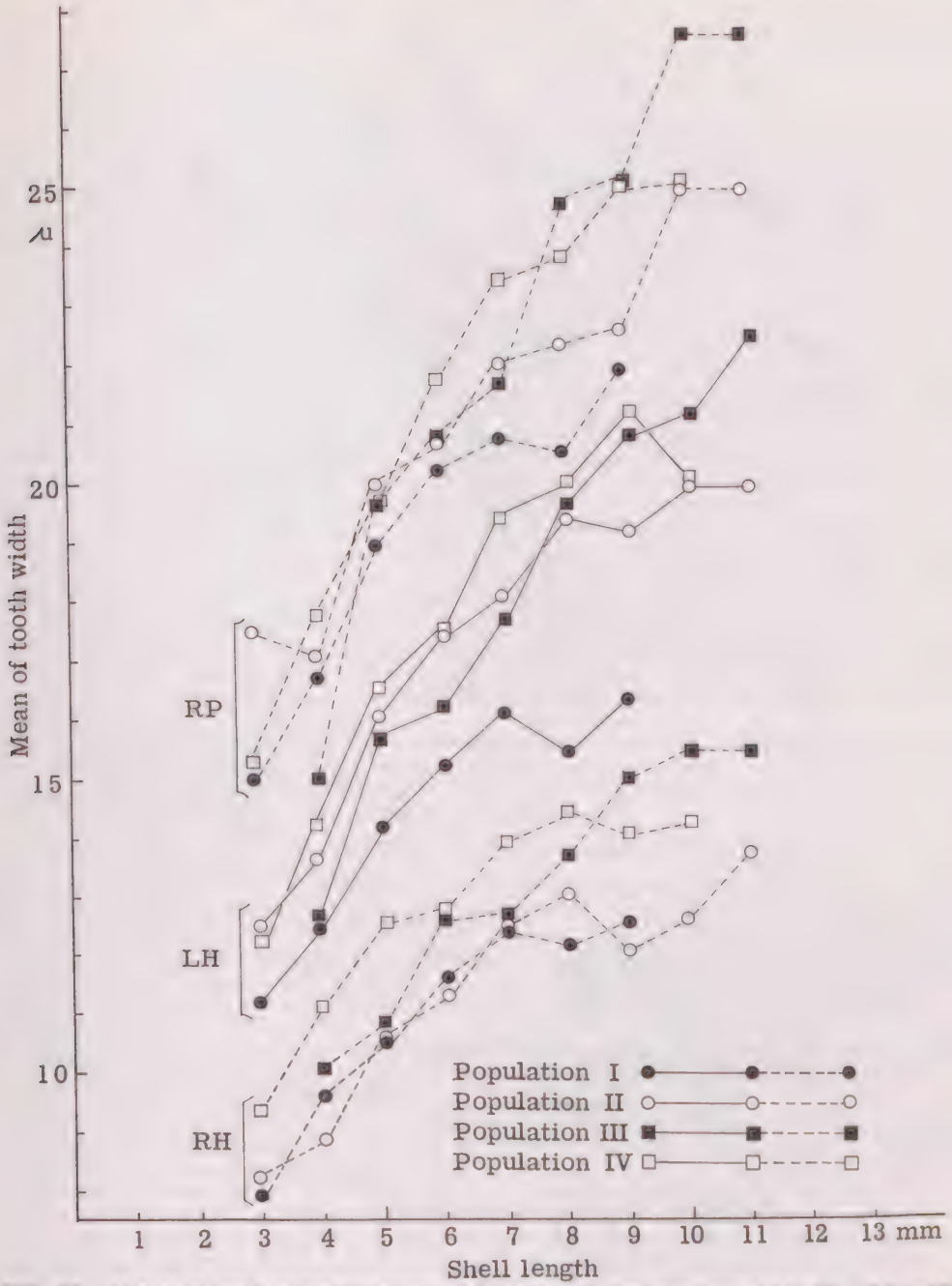
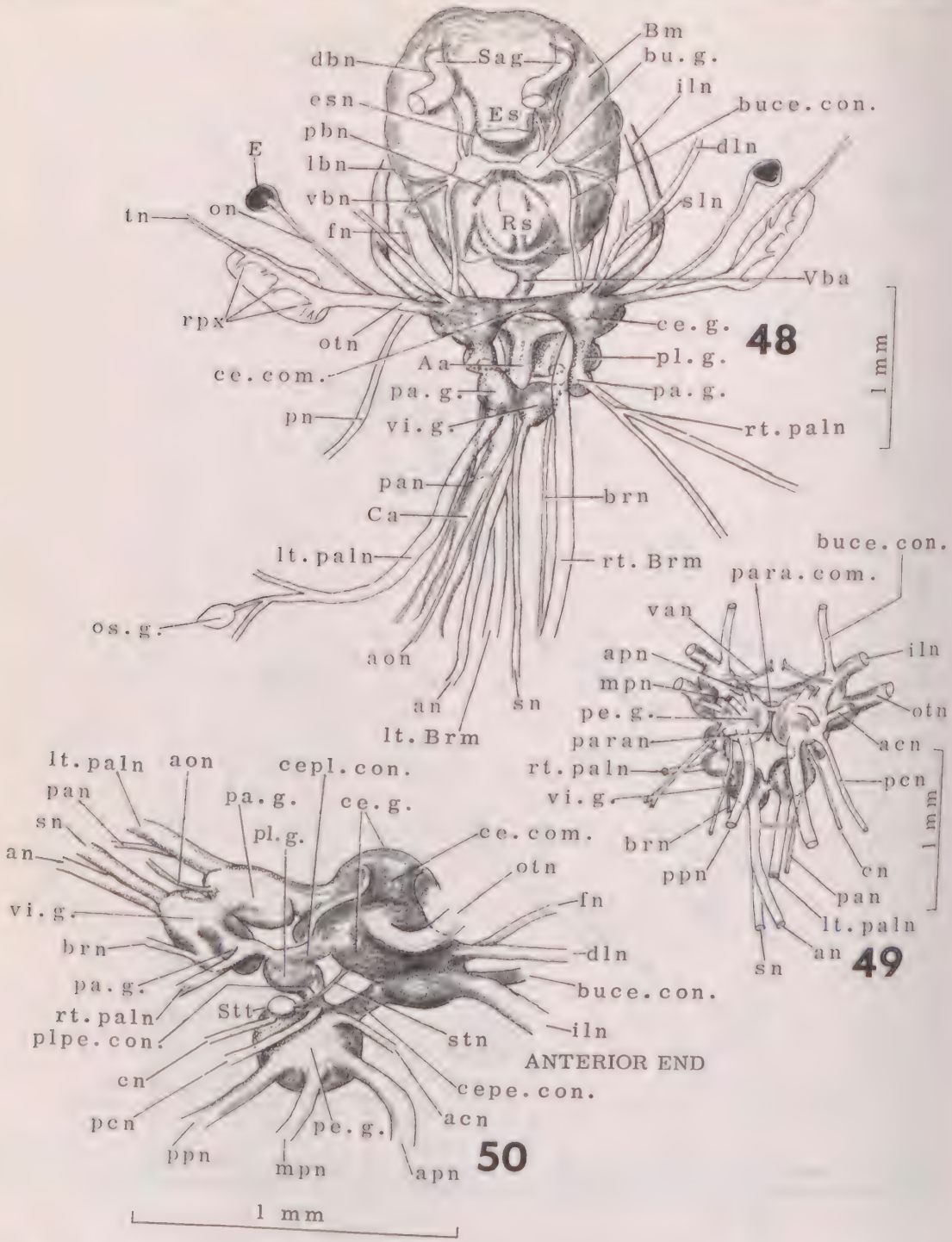


FIG. 47. Means of tooth widths in relation to size group, for populations I to IV. (RP, width of the posterior side of rachidian tooth; RH, width of rachidian hook-body; LH, width of hook-body of L1).

IV. Nervous System

1. General Morphology

The central nervous system of *Bulinus* has 4 pairs of symmetrical ganglia (buccal, cerebral, pedal and pleural), 1 pair of asymmetrical ganglia (parietal) and a single visceral (or abdominal) ganglion. Of these ganglia, 9, excepting the buccal ganglia, compose the circum-esophageal nerve ring (Fig. 48) which encircles the esophagus at its narrowest portion. These ganglia are separated from one another by commissures and connectives. A further peripheral ganglion, osphradial ganglion (os.g.), is situated deep in the tissue of the mantle roof where it connects to the neck and at the right side of the entrance of the pallial



FIGS. 48-50. Central nervous system and peripheral nerves of *Bulinus tropicus*. 48, Dorsal view; 49, Ventral view; 50, Anterior half is a lateral view and posterior half is a slightly dorsolateral view, from the right side.

Aa, aortic arborescence; acn, anterior cervical nerve; an, anal nerve; aon, aortic nerve; apn, anterior pedal nerve; Bm, buccal mass; Brm, buccoretractor muscle; brn, buccoretractor nerve; buce.con., buccocerebral connective; bu.g., buccal ganglion; Ca, cephalic artery; ce.com., cerebral commissure; ce.g., cerebral ganglion; cepe.con., cerebropedal connective; cepl.con., cerebropleural connective; cn, columellar nerve; dbn, dorsobuccal nerve; dln, dorsolabial nerve; E, eye; Es, esophagus; esn,

cavity. The ganglia, commissures, connectives, and principal peripheral nerves together with their courses and distributions, which were identical in the 4 populations, are given below and illustrated for *B. tropicus*. The variable terminology applied to the peripheral nerves is compared in Table 14.

A. Cerebral ganglia, commissure, connective and principal nerves (Figs. 48-50)

The cerebral ganglia (ce.g.) are large, bilobed, paired ganglia which lie on both sides of the narrowest portion of the esophagus. They are connected dorsomedially by a fairly long and thick intercerebral commissure (ce.com.). The ganglia are also connected anteriorly to the buccal ganglia (bu.g.) by long, thin buccocerebral connectives (buce.con.), ventrally to the pedal ganglia (pe.g.) by a short cerebropedal connective (cepe.con.) and ventroposteriorly to the pleural ganglia (pl.g.) by a short cerebropleural connective (cepl.con.). The cerebral ganglia issue the 5 paired and a single peripheral nerve described below.

(1) Ventrobuccal arterial nerve (van, paired): a fine nerve which originates at the ventroanterior portion of the ganglia where it is ventral to the base of buccocerebral connective. This nerve proceeds medially and supplies the ventrobuccal artery (Vba) and aortic arborescence (Aa).

(2) Superior labial nerve (sln, paired): a rather thick nerve which originates from the anterior portion of the ganglia, where it is dorsal to the base of buccocerebral connective (buce.con.). This nerve may proceed together with the inferior labial nerve (iln) and then separate after a short distance. It divides into a frontal nerve (fn) which proceeds dorsally and innervates the dorsal wall anterior to the eye and the main dorsolabial nerve (dln) which proceeds anteriorly and supplies the dorsal part of labium.

(3) Inferior labial nerve (iln, paired): a stout and thick nerve which originates from the ventroanterior process of ganglia. It proceeds lateroanteriorly and gives off 2 branches to supply the outer portions of the velum while the main nerve supplies the part of the labium ventral to the mouth.

(4) Penial nerve (pn, single, left only): a stout nerve which originates at the ventroanterior process of the left cerebral ganglion where it is just ventral to the left inferior labial nerve. It proceeds laterally and turns posteriorly with the penial artery. It innervates the penial complex, penetrating where the penial retractor muscle attaches.

(5) Optic-tentacular nerve (otn, paired): a stout and thick nerve which originates from the dorsolateral process of the ganglia. It proceeds laterally and gives off the optic nerve (on) which supplies the eye. The main nerve proceeds further to the "rhinophore" (Demian, 1960) where it gives off several short and thick branches to form the rhinophoral plexus (rpx). The main nerve further penetrates into the tentacle as the tentacular nerve (tn).

(6) Statocyst nerve (stn, paired): an extremely thin nerve which originates between the roots of the cerebropedal (cepe.con.) and cerebropleural (cepl.con.) connectives. It runs posteriorly around the pleuropedal connective (plpe.con.) and finally reaches the statocyst (Stt) which is a shiny spherical organ, located on the dorsoposterior portion of the pedal ganglia (pe.g.).

B. Pedal ganglia, commissures, connectives and peripheral nerves (Figs. 49-50)

The pedal ganglia (pe.g.) are medium-sized, paired ganglia which lie ventrally to the esophagus. The ganglia are connected to each other by 2 inter-pedal commissures: a pedal commissure at the mid-dorsal part of the ganglia and a parapedal commissure (para.com.) at the ventroanterior portion of the ganglia. The pedal ganglia connect dorsally on each side to the cerebral ganglia by the cerebropedal connectives (cepe.con.), and dorsoposteriorly to the pleural ganglia by the pleuropedal connectives (plpe.con.). The pedal ganglia issues the 6 pairs of peripheral nerves listed below, while a 7th single nerve arises from the parapedal commissure.

(1) Anterior cervical nerve (acn): a medium-sized nerve which originates on the pedal ganglion laterally near the base of the cerebropedal connective (cepe.con.). It proceeds laterally and branches off to supply the skin of the lateral side of head region.

(2) Posterior cervical nerve (pcn): a medium-sized nerve which originates laterally near the base of the pleuropedal connective (plpe.con.). It proceeds lateroposteriorly, branches off and penetrates the skin posterior to the opening of the preputium.

(3) Columellar nerve (cn): a medium-sized nerve which originates ventrally of the statocyst (Stt). It proceeds ventroposteriorly to supply the origin of the columellar muscles.

(4) Anterior pedal nerve (apn): a thick nerve which originates on the ventroanterior part of the ganglia. It proceeds ventroanteriorly and branches off before penetrating the deep layer of foot tissue. The branch

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esophageal nerve; fn, frontal nerve; iln, inferior labial nerve; lbn, laterobuccal nerve; lt., left; mpn, median pedal nerve; on, optic nerve; os.g., osphradial ganglion; otn, optic-tentacular nerve; pa.g., parietal ganglion; paln, pallial nerve; pan, parietal nerve; para.com., parapedal commissure; paran, parapedal nerve; pbn, postbuccal nerve; pcn, posterior cervical nerve; pe.g., pedal ganglion; pl.g., pleural ganglion; plpe.con., pleuropedal connective; pn, penial nerve; ppn, posterior pedal nerve; rpx, rhinophoral plexus; Rs, radular sac; rt., right; Sag, salivary gland; sln, superior labial nerve; sn, splanchnic nerve; stn, statocyst nerve; Stt, statocyst; tn, tentacular nerve; van, ventrobuccal arterial nerve; Vba, ventrobuccal artery; vbn, ventrobuccal nerve; vi.g., visceral ganglion.

which penetrates the foot runs lateroanteriorly to supply the corresponding portion of the foot. The other branch proceeds anteriorly along the connective tissue lining of the cephalic cavity to supply the medioanterior portion of the foot.

(5) Median pedal nerve (mpn): a nerve slightly thinner than the anterior pedal nerve (apn) which originates at the midventral part of the ganglia. It proceeds ventrolaterally and penetrates the foot to supply the latter part of the anterior half of the foot.

(6) Posterior pedal nerve (ppn): the thickest nerve among the pedal nerves, which originates at the ventroposterior part of the ganglia. The main nerve branches within the foot tissue as it proceeds posteriorly. All branches of this nerve supply the entire posterior half of the foot.

(7) Parapedal nerve (paran): an extremely fine single nerve originating on the parapedal commissure (para.com.). After emerging from the commissure, this nerve proceeds ventrally to supply the columellar muscle.

C. Pleural ganglia and connectives (Figs. 48, 50)

The pleural ganglia (pl.g.) are small, symmetrical paired ganglia which lie on the sides of the esophagus, posterior to the cerebral and pedal ganglia. They connect on each side dorsoanteriorly to the cerebral ganglia (ce.g.) by the cerebropleural connective (cepl.con.), and ventroanteriorly to the pedal ganglia (pe.g.) by the pleuroparietal connectives (plpe.con.). The pleural ganglia issue no peripheral nerves.

D. Parietal ganglia, connectives and peripheral nerves (Figs. 48-52)

The parietal ganglia (pa.g.) are paired ganglia of different sizes, the left ganglion being larger than the right one. The right parietal ganglion is about the same size as the pleural ganglion, while the larger left parietal ganglion is about the size of the visceral ganglion (vi.g.). The parietal ganglia connect on each side anteriorly to the pleural ganglia by the pleuroparietal connectives. The right parietal ganglion is joined mediposteriorly to the visceral ganglion (vi.g.) by a rather long parietovisceral connective. The left parietal ganglion connects medially to the visceral ganglion by an extremely short parietovisceral connective (pavi.con.). The right parietal ganglion issues 1, the left parietal ganglion 3 peripheral nerves.

Right parietal ganglion

Right pallial nerve (rt.paln): a thick nerve which originates from the dorsoposterior portion of the ganglion. It proceeds dorsoposteriorly and divides into the anterior and posterior branches. The anterior branch penetrates the muscle layer and proceeds anteriorly to supply the right side of the anterior mantle skirt (collar). The posterior branch proceeds posteriorly to supply the right side of the posterior mantle skirt.

Left parietal ganglion

(1) Left pallial nerve (lt.paln): a thick and stout nerve which originates at the posterior portion of the ganglion. It proceeds dorsoposteriorly to the medial corner of the pneumostome, where it divides into 2 nerves: (a) a lateral nerve supplying the left side of the anterior mantle skirt, and (b) a medial nerve which also divides into 2 branches after a short distance. The medial branch supplies the central portion of the anterior mantle skirt and the lateral branch ends up at the osphradial ganglion (os.g).

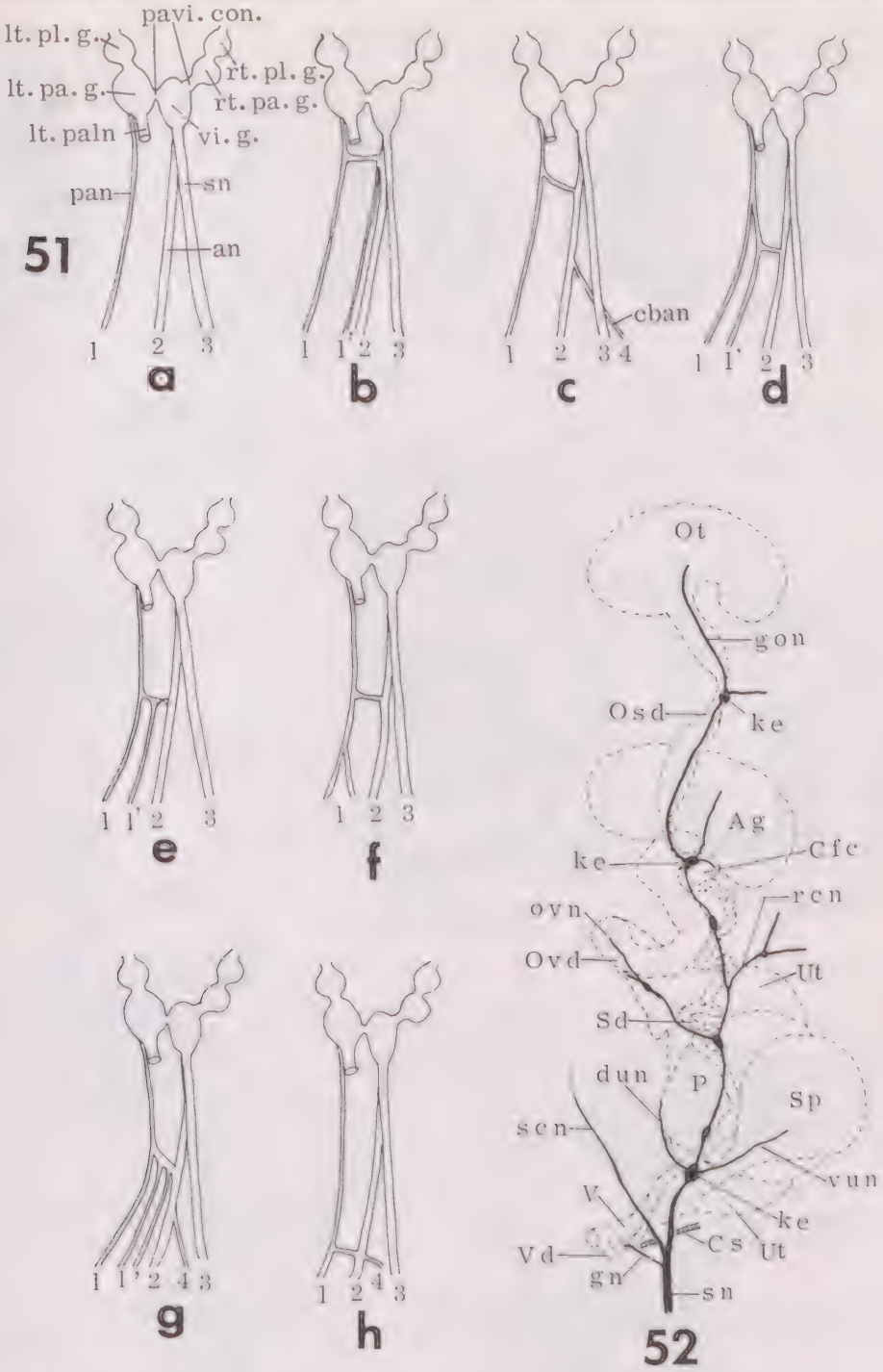
(2) Parietal nerve (pan): a thin nerve which originates at the ventroposterior portion of the ganglion. It proceeds posteriorly below the left pallial nerve (lt.paln) and anastomoses, in most specimens, with the anal nerve (an). Before anastomosing, 2-3 nerves branch from it; these supply the body wall and muscles near the female opening. The patterns of anastomosing and branching are variable (Figs. 51, b-h). In rare cases, it does not anastomose with the anal nerve (Fig. 51a).

(3) Aortic nerve (aon, Fig. 48): a fine nerve which originates on the posterior portion of the ganglion, medial to the origin of the left pallial nerve (lt.paln). It proceeds dorsoposteriorly along the cephalic artery (Ca) to supply the cephalic septum (Cs, Fig. 52) which separates the cephalic and visceral hemocoels.

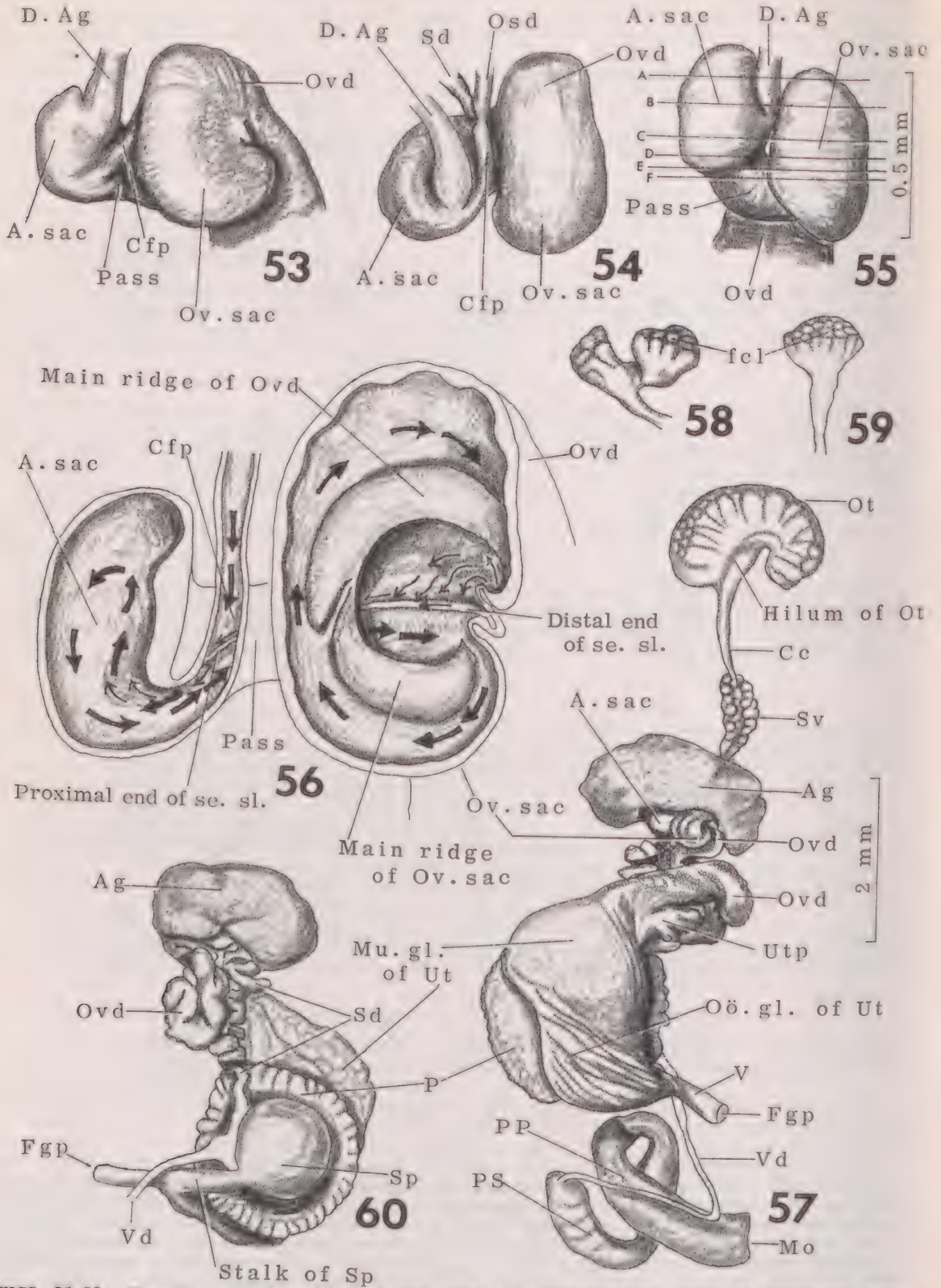
E. Visceral ganglion, connectives and peripheral nerve (Figs. 48-52)

The visceral ganglion (vi.g.) is a large, oval and unpaired ganglion which lies ventral to the esophagus. The connectives with the visceral ganglion have already been described in Section D (Fig. 51a). The ganglion issues 3 peripheral nerves listed below.

(1) Splanchnic nerve (sn, Fig. 52): a thick and stout nerve which originates at the posterior end of the ganglion (Figs. 48-50). It proceeds posteriorly and gives off a short nerve, the genital nerve (gn), on the right to supply the vas deferens (Vd). The main nerve divides into a dorsal main nerve and a ventral columellar nerve (scn) before penetrating the cephalic septum (Cs). The columellar nerve (scn) runs over the middle of the columellar muscle. The main nerve spreads over the reproductive organs and shows many knotty enlargements (ke). The first such knotty enlargement lies near the distal portion of the uterus on the ventral side. It gives off 2 branches in opposite directions. The left branch, the ventrouterine nerve (vun), supplies the spermatheca (Sp), prostate (p) and ventral side of the uterus (ut), while the right branch, the dorsouterine nerve (dun), supplies to the dorsal portion of the uterus (ut). The main nerve proceeds posteriorly along the sperm duct (Sd) and gives off a right branch, the oviducal nerve (ovn), which goes to the uterine pouches and the oviduct, and a left branch, the renocardial nerve (rcn), which further branches to supply the heart and kidney. The main nerve follows the sperm duct to the carrefour complex (Cfc). The knotty enlargement of the splanchnic nerve lying between the ovisperm duct, sperm



FIGS. 51-52. Nervous system of *Bulinus tropicus*, semidiagrammatic. 51, Patterns of anastomosing of parietal nerve with anal nerve, dorsal view (1, parietal nerve; 1', branches of parietal nerve; 2, anal nerve; 3, splanchnic nerve; 4, columellar branch from anal nerve); 52, Splanchnic nerve, ventral view. Ag, albumen gland; an, anal nerve; cban, columellar branch from anal nerve; Cfc, carrefour complex; Cs, cephalic septum; dun, dorsouterine nerve; gn, genital nerve; gon, gonadal nerve; ke, knotty enlargement; lt., left; Osd, ovispermduct; Ot, ovotestis; Ovd, oviduct; ovn, oviducal nerve; P, prostate gland; pa.g., parietal ganglion; paln, pallial nerve; pan, parietal nerve; pavi.con., paritovisceral connective; pl.g., pleural ganglion; rcn, renocardial nerve (a branch from splanchnic nerve); rt., right; scn, columellar nerve (a branch from splanchnic nerve); Sd, sperm duct; sn, splanchnic nerve; Sp, spermatheca; Ut, uterus; V, vagina; Vd, vas deferens; vi.g., visceral ganglion; vun, ventrouterine nerve.



FIGS. 53-55. Carrefour complex of *Bulinus sericinus*. 53, Dorsoposterior view; 54, Posterior view; 55, Left side view. Transverse lines A, B, C, D, E and F corresponding to sections shown in Figs. 67-72. Scale line at Fig. 55.

duct and oviduct gives off the nerves which supply the carrefour complex and albumen gland (Ag). The main nerve further follows the ovisperm duct (Osd) to its middle portion where a knotty enlargement gives off a branch which anastomoses with the gastric plexus of the stomach. The main nerve arising there, the gonadal nerve (gon), proceeds to supply the ovotestis (Ot).

(2) Anal nerve (an): a thick, stout nerve (median pallial nerves of other authors, see p 157, Table 13) which originates at the posterior end of the ganglion, just ventral to the splanchnic nerve (sn). This nerve has been called the "median pallial nerve" (Demian, 1960) before it anastomoses with the parietal nerve (see above) and the "internal pallial nerve" after anastomosing. It proceeds posteriorly toward the left side and may give off a small branch to supply the columellar muscle (4, Figs. 51c, g, h), while the main nerve passes ventral to the vagina and vas deferens near the female opening and proceeds to the ventral side of the rectum. Along its course it gives off several branches to supply the anus, rectum and pseudobranch. Finally, the main nerve reaches the posterior corner of the mantle skirt.

(3) Buccoretractor nerve (brn): a medium to fine nerve which originates on the right lateroanterior portion of the visceral ganglion. It proceeds posteriorly and supplies the buccal retractor muscle.

F. Buccal ganglia, commissure, connective and peripheral nerves (Fig. 48)

The buccal ganglia (bu.g.) are small paired ganglia which lie at the dorsoposterior part of the buccal mass (Bm), dorsal to the radular sac (Rs) and ventral to the esophagus (Es). The ganglia connect with each other by a rather long buccal commissure and with the cerebral ganglia (ce.g) by a long buccocerebral connective (buce.con.). Each ganglion issues the 5 peripheral nerves listed below.

(1) Esophageal nerve (esn): a fine nerve which originates from the dorsomedial side of the ganglion. It proceeds dorsally and divides into the anterior and posterior esophageal nerves which supply the esophagus, extending as far as the posterior end of the esophagus.

(2) Dorsobuccal nerve (dbn): a fine nerve which originates from the dorsolateral side of the ganglion. It proceeds dorsoanteriorly along the salivary gland (Sag) and divides into a dorsal branch, which passes over the salivary gland to supply the dorsal portion of the buccal cavity, while a ventral branch penetrates into the deep layer of the buccal mass to supply its dorsolateral portion.

The above 2 nerves sometimes originate together from the buccal ganglion and branch after a short distance.

(3) Laterobuccal nerve (lbn): a fine nerve which originates at the lateral side of the ganglion. It proceeds anteriorly and penetrates deeply into the buccal mass to supply its lateral portion.

(4) Ventrobuccal nerve (vbn): a fine nerve which originates at the lateral side of the ganglion. It proceeds ventroanteriorly and, at the insertion of the buccal retractor muscle, penetrates the deep layers of the buccal mass and branches to supply the ventroposterior portion.

(5) Postbuccal nerve (pbn): an extremely fine nerve which originates at the buccal commissure near the base of each ganglion. It proceeds ventrally and penetrates the deep leayer of the buccal mass to supply its posterior portion and the radular sac.

V. Reproductive System

1. General Morphology

Ovotestis. The ovotestis (Ot, Fig. 57) is partly embedded in the digestive gland and may be either spirally coiled toward the tip of the shell (Figs. 80a, 81a) or completely embedded in the digestive gland, not reaching the tip of the shell (Fig. 59). In most specimens it is formed by a single lobe, but occasionally bilobed ovotestes (Fig. 58) were observed. Each ovotestis consists of different numbers of follicles (fcl) or tubules (Figs. 58, 59), depending on the age and physiological state of each individual snail. The ovotestis is white in smaller snails (less than 6.4 mm shell length) and yellowish in larger, more mature adult snails (longer than 6.5 mm). All the follicles converge into a transparent collecting canal at the hilum of the organ (Fig. 57).

Histologically, all stages of spermatogenesis and oögenesis can be observed in the same tubule; and

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FIG. 56. Cross-section of carrefour complex. Semidiagrammatic, showing internal structure and possible direction of foreign sperm migration (thin arrows) and movement of the fertilized albumen coated ova (bold arrows).

FIG. 57. Whole reproductive system of *Bulinus tropicus*. Snail shell length 9 mm, dorsal view.

FIG. 58. Bilobed ovotestis of *Bulinus sericinus*.

FIG. 59. Part of ovotestis of *Bulinus tropicus*.

FIG. 60. Reproductive system of *Bulinus tropicus* with hermaphrodite system and penial complex removed, ventral view. (Same snail as Fig. 57).

Ag, albumen gland; A.sac, albumen sac; Cc, collecting canal of ovotestis; Cfp, carrefour pouch; D.Ag, duct of albumen gland; fcl, follicles of ovotestis; Fgp, female genital pore; Mo, male opening; Mu.gl., muciparous gland of uterus; Oö.g., oöthecal gland of uterus; Osd, ovispermduct; Ot, ovotestis; Ov.sac, oviducal sac; Ovd, oviduct; P, prostate gland; Pass, passage; PP, preputium; PS, penial sheath; Sd, sperm duct; se.sl., "seminal slot"; Sp, spermatheca; Sv, seminal vesicle; Ut, uterus; Utp, uterine pouch; V, vagina; Vd, vas deferens.

young oöcytes (Oöc) (Fig. 63), spermatids (Spd) and sperm (Figs. 63, 65) are largely confined to the lower portion of the tubule, while the upper portion is occupied by maturing oöcytes, as many as 6 per tubule (Fig. 61).

Both ovotestis and the digestive gland are covered by a thin membrane, the tunica propria, which has some black pigment where it covers the ovotestis.

Ovispermduct. The ovispermduct (Osd) runs from the collecting canal of the ovotestis to the carrefour complex along the columellar face of the digestive gland, then it passes between the left side of the gizzard and the concave face of the albumen gland (Ag). Morphologically, a sharp constriction is seen between the collecting canal of the ovotestis and the ovispermduct. The ovispermduct can be subdivided into 2 regions: a proximal opaque duct with tuberculated enlargements (Sv, Fig. 57), which is a functionally differentiated seminal vesicle, and a distal thin duct which runs to the carrefour complex.

Carrefour complex (Figs. 53-56, 67-72). The carrefour complex is located at the hilum of the albumen gland and consists of an albumen sac (A.sac) i.e., a dilation at the distal end of the duct of albumen gland, an oviducal sac (Ov.sac) i.e., a dilation at the end of the oviduct, a passage (Pass) between the 2 sacs and the carrefour pouch (Cfp). This small pouch (Figs. 53-54, 67-70) is located dorsal to the passage; the ovisperm duct (Osd) ends before entering it and the sperm duct (Sd) originates from it (Fig. 54). The carrefour pouch (Cfp), as well as the proximal end of the seminal groove or "slot" (se.sl., Figs. 56, 70), leads into the oval albumen sac (A.sac) located posteroventrally at the right side of the complex. The duct of the albumen gland (D.Ag), after leaving the gland, opens into the medial wall of the albumen sac at about 1/3 the distance from the vertex of the albumen sac (Figs. 53-55, 68). Histologically, the medial wall of the albumen sac is lined with ciliated columnar cells while the lateral wall is lined with cuboidal ciliated cells (Figs. 67-72). The albumen sac is surrounded by 4-6 layers of muscle fibers and connective tissue.

The oviducal sac (Ov.sac) is located dorsoanteriorly and on the left side of the complex. It is formed by a 180 degree bend of the proximal end of the oviduct. The main ridge (Fig. 56) in the oviducal sac, together with that of the oviduct, arch over the passage and "seminal slot" at the bend. The sac is lined with ciliated columnar cells.

The deep groove, which has been called the "seminal slot" by Walter, (1968), extends from a small triangular pouch into the albumen sac (Fig. 56) at the bend of the oviduct. It probably is a passage for foreign sperm.

Male system

Sperm duct. The sperm duct (Sd, Figs. 54, 60) is a whitish duct which originates from the carrefour pouch and is a continuation of the ovisperm duct. It is extremely convoluted and runs (in ventral view) along the right side of the oviduct to the central part of the prostate gland (P).

Prostate gland. The prostate gland (P, Fig. 60) is a white organ, discoidal in shape, with a concave face on the ventral side and a slightly convex face on the dorsal side. It fits into a depression of the ventral floor of the uterus and lies between the latter and the spermatheca (Sp).

Vas deferens. Leading out from the central part of the prostate gland (P, Fig. 60) is the vas deferens (Vd), which runs (ventral view) along the left side of the duct of the spermatheca (Sp) and the vagina. Then, it crosses the vagina (V) and becomes embedded into the body wall anterior to the female genital pore (Fgp, Fig. 57). At a point slightly posterior to the male opening (Mo), it emerges from the body wall and back tracks along the side of the preputium (PP) of the usually U-shaped penial complex to enter the proximal end of the penial sheath.

Penial complex. The penial complex (Fig. 57) consists of the proximal penial sheath (PS) and a distal preputium (PP). The penial sheath (PS) lodges the epiphallus and the retracted penis within (Figs. 73-74). According to its structure, the penial sheath can be subdivided into a proximal membranous and a distal muscular portion. The distinction is also shown in cross sections of Demian's figures (1960; pl. 7: membranous sheath, figs. 27 E, F; muscular sheath, figs. 27 B, C). The membranous sheath contains an extremely thin, coiled and convoluted epiphallus, followed by a dilated penis of varying diameter (Fig. 74). The muscular sheath is shiny and may assist functionally in propelling the sperm during ejaculation. The sheath encloses a cavity, the penial hemocoel. This hemocoel can also be observed in an expanded state during penial eversion and copulation (Fig. 76). During penial retraction, the dilated duct adjacent to the thin epiphallus is lined with a folded luminal epithelium having many papillae (Fig. 74). During copulation, this portion everts and the papillae can be seen on the external surface (Figs. 75-77). This portion, inserted in the female genital system, was seen to expand greatly (in *B. natalensis*), exactly fitting the shape of the uterus, with the tip of the penis reaching one of the uterine pouches (Fig. 77).

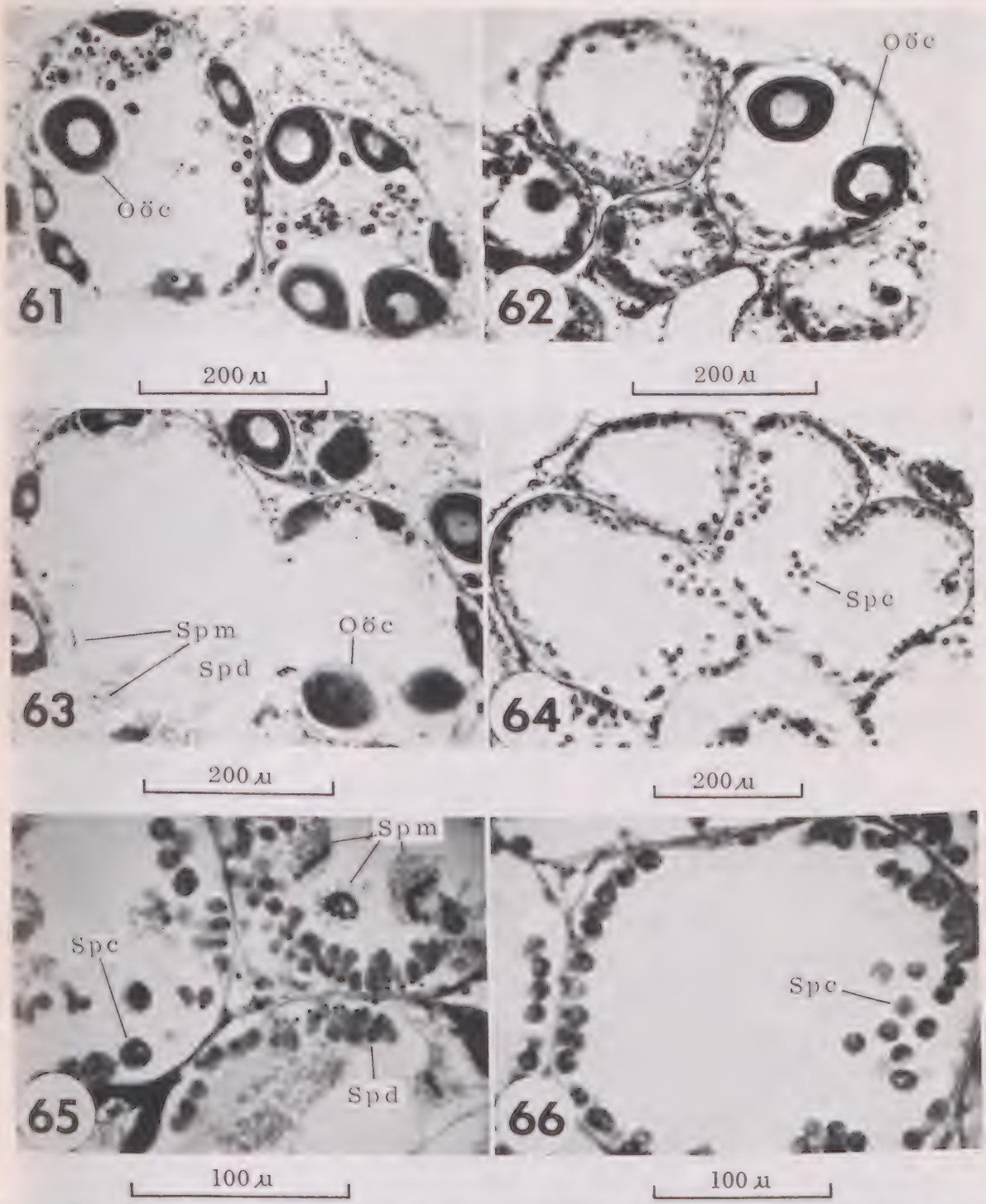
Two pilasters are observed in cross sections of the preputium, one on the ventroanterior corner and the other at the dorsoposterior corner. These pilasters are present along the whole length of the preputium, but they gradually disappear as they proceed toward the proximal end (Hubendick, 1948; Wright, 1957).

In its normal, non everted, position, the penial complex is situated in the left side of the cephalic cavity, behind the buccal mass and is usually curving in a U-shape.

Female System

Oviduct. The oviduct (Ovd, Fig. 60) leads out from the carrefour complex at the oviducal sac or bend (crook). It proceeds toward the uterus and makes 2-3 loops.

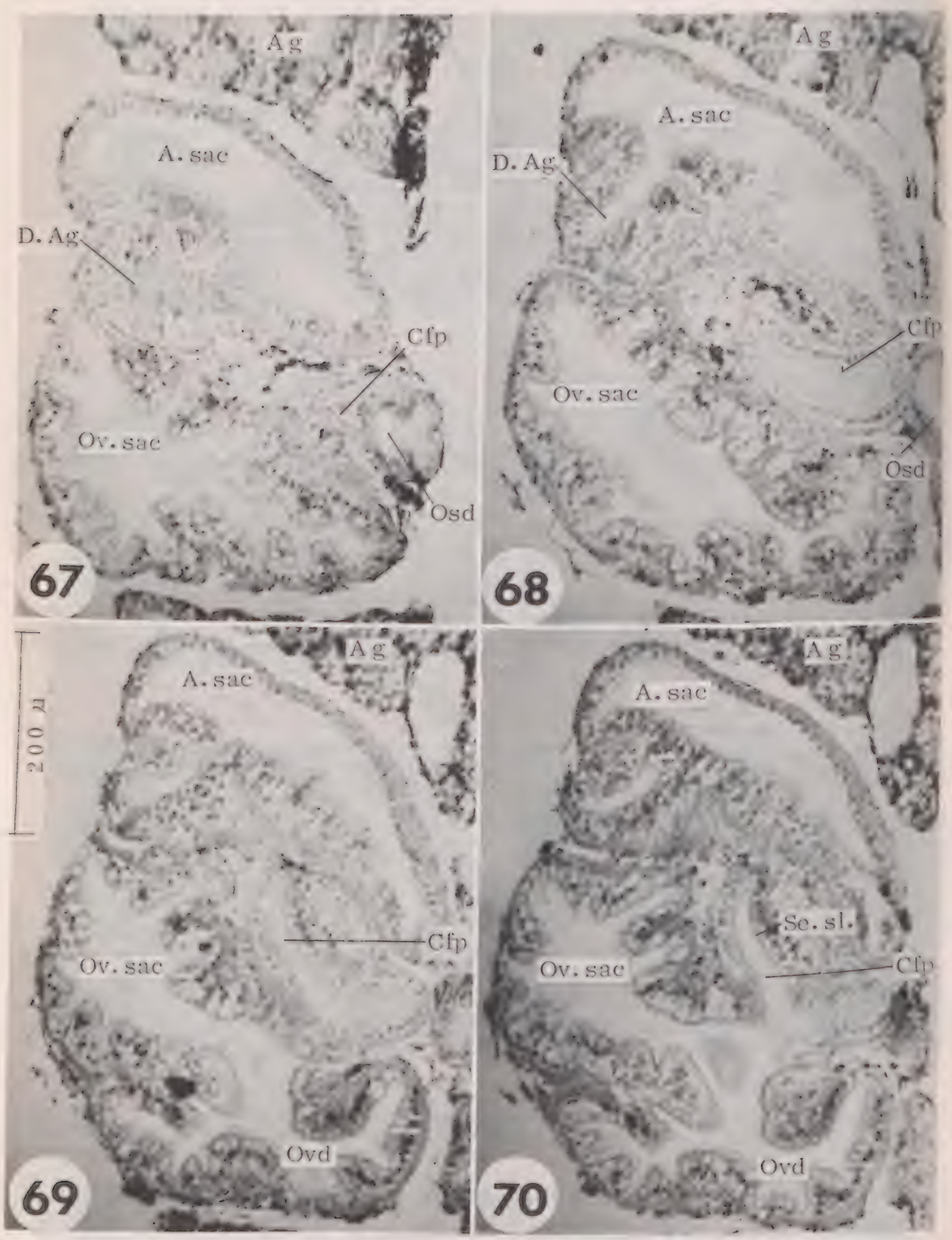
Uterus. At the entrance of the oviduct into the uterus, irregular uterine pouches (Utp, Fig. 57) surround the oviduct on the left (right side of figure) and ventral side of the animal. From the entrance, longitudinal folds run on the left side of the uterus toward the vagina (V). To the right of these longitudinal folds there



FIGS. 61, 63, 65. Cross sections of ovotestis of *Bulinus truncatus*. 61, Proximal portion of tubules, showing 5-6 maturing oöcytes in each tubule; 63, Distal portion of tubules, showing sperm, spermatids and oöcytes; 65, Enlargement of distal portion of tubules, showing spermatocytes (Spc), sperm (Spm) and spermatids (Spd).

FIGS. 62, 64, 66. Cross sections of ovotestis of sterile F_1 progeny between *Bulinus hexaploidus* and the albino strain of *Bulinus tropicus*. 62, Proximal portion of tubules, showing 1-2 maturing ova in each tubule; 64, Distal portion of tubules, showing spermatocytes only; 66, Enlargement of distal portion of tubules, showing spermatocytes only.

Oöc, oöcyte; Spc, spermatocyte; Spd, spermatid; Spm, sperm.


Ag
A. sac
D. Ag
Cfp
Ov. sac
Osd
67
Ag
A. sac
D. Ag
Cfp
Ov. sac
Osd
68
200 µ
Ag
A. sac
Cfp
Ov. sac
Ovd
69
Ag
A. sac
Se. sl.
Ov. sac
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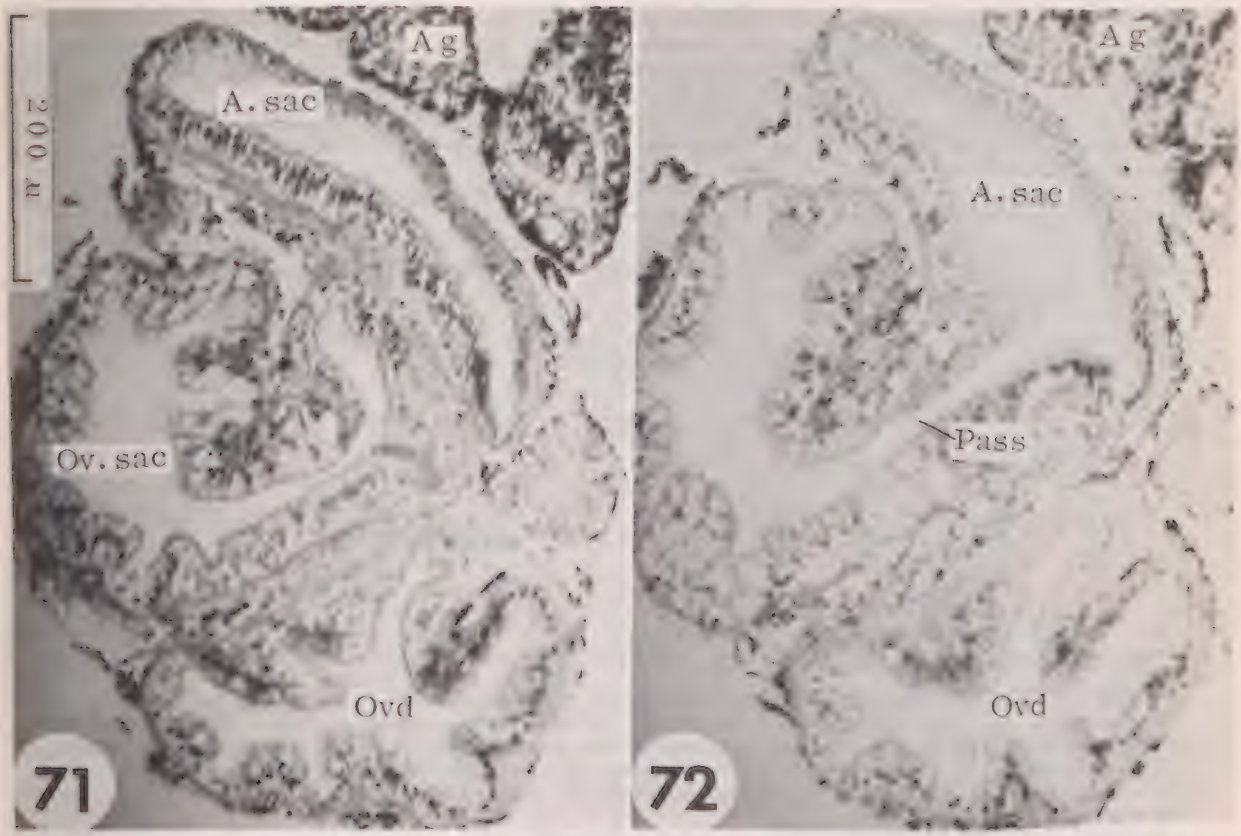


FIGS. 67-72. Cross sections through different levels (see A-F, Fig. 55) of the carrefour complex of *Bulinus sericinus*.

Ag, albumen gland; A.Sac, albumen sac; Cfp, carrefour pouch; D.Ag, duct of albumen gland; Osd, ovisperm duct; Ovd, oviduct; Ov.sac, oviducal sac; Pass, passage; Se.Sl., "seminal slot."

are, externally: (1) a translucent colorless or yellowish triangular area, the muciparous gland (Mu.gl.); (2) an opaque, diagonally striated area, the oöthecal gland of the uterus (Oö.gl.). Internally, the muciparous region is composed of a cluster of tubules which open separately into the flat uterine cavity from the dorsal side. The oöthecal region is deeply folded, the folds converging towards the vagina (V). The ventral wall of the uterus has rather low folds which also converge toward the vagina, as do those of the oöthecal region.

Spermatheca. The spermatheca (Sp, Fig. 60) is a sac opening into the vagina by means of a stalk. The shape and size of the spermatheca and the length of its stalk vary according to the age and physiological condition of the individual snail at the time of fixation (see Figs. 78b-100b), the sac varying in shape from rod-like to bulbous.

Vagina. The vagina (V, Fig. 57) is a short internally folded duct leading from the uterus to the exterior. The folds are the continuation of those from the oöthecal region, the ventral wall and the left side of the uterus.

Female genital pore. The female genital pore (Fgp, Figs. 57, 60) lies on the left side of the neck, just below the pseudobranch. The pore is usually slightly elevated above the surrounding skin, like a small papilla.

2. Comparison of Species

Population I (*Bulinus tropicus*, n=18). Figs. 57, 60, 78-81

All 26 specimens examined were euphallic.

Snails of 3 mm shell length (Figs. 78, a-b). The ovotestis was large, but not yet differentiated. The ovisperm duct was long and smooth and did not yet show seminal vesicle enlargements in its lower portion. The primordium of the albumen gland was a small digitated or lobed structure. The oviduct could be clearly distinguished from the uterus-vagina complex by a constriction. The spermatheca was rod-like. The male duct was already clearly defined. The penial complex had a U-bend at its proximal end; however, the penial sheath and preputium were not clearly differentiated.

Snails of 4.5 mm shell length (Figs. 79, a-b). The general structure was the same as that of the 3 mm

snail. However, the upper half of the ovisperm duct had the seminal vesicle enlargements. The prostate gland was extremely enlarged. The oviducal crook appeared. The oöthecal and muciparous regions of the uterus began to appear, but no uterine pouches were observed. The spermathecal sac was clavate.

Snails of 6, 7.5 and 9 mm shell length (Fig. 80-81, a-b; 57, 60). For snails with shells 6 mm or longer, the general structure was exactly as that described in the previous section of general morphology. The spermatheca changed from clavate (Fig. 79b) to oval (Fig. 80b) and spherical (Figs. 60, 81b). The albumen gland greatly increased in size.

Relationship of organ sizes. The size relationship between the ovotestis and albumen gland during growth was as follows: at 3 mm shell length the ovotestis was very much larger than the albumen gland. As the snails grew, the ovotestis enlarged more slowly than the albumen gland. In snails with shells 6-9 mm in length, the ovotestis was about the same size as the ablumen gland, and in those longer than 9 mm, the ovotestis was smaller than the albumen gland.

The prostate gland (P) was initially larger than the albumen gland (Ag) and spermatheca (Sp), which in mature snails reached approximately the same size (=area, ventral view). The relationships between the sizes of these organs for 5 shell size groups are tabulated as follows:

Shell size group (mm)	Ag : P	Sp : P
4	1 : 5	1 : 8
5	1 : 5	1 : 8
6	1 : 2-8	1 : 3-8
7	1 : 1-4	1 : 1-5
8	1 : 1	1 : 1

Population II (*Bulinus truncatus*, n=36). Figs. 82-90

Among 118 specimens dissected, 18 specimens (15.2%) were euphallic and the rest were aphallic.

Snails of 3 mm shell length (Figs. 82-83). Aphallic specimens (Figs. 82, a-b): The ovotestis was sponge-like tissue that had no follicular structure at this stage. The ovisperm duct was long and smooth, without the seminal vesicle enlargements in its upper half. The primordium of the albumen gland was a lobed projection. The oviducal crook and oviduct could be distinguished from the uterus-vagina complex. The spermatheca was small and rod-like.

Euphallic specimens (Figs. 83, a-b): In a specimen 3.6 mm in shell length, the ovotestis already had a differentiated follicular structure. The ovisperm duct was long and smooth. The uterus-vagina complex was still an undifferentiated tube. The male duct and prostate were distinct. The penial complex had a U-bend near its proximal end.

Snails of 4.5 mm shell length (Figs. 84-85). Aphallic specimen (Figs. 84, a-b): This specimen was 4.6 mm in shell length. The ovotestis was extremely large and follicular in structure. In the upper half of the ovisperm duct the seminal vesicle enlargements were present. The oviducal crook was distinct. The oöthecal and muciparous regions of the uterus had begun to differentiate. No uterine pouches were observed. The spermatheca was slightly clavate. The proximal end of the vas deferens was enlarged and transparent.

Euphallic specimen (Figs. 85, a-b): This specimen was 4.3 mm in shell length. The general reproductive structures were like those of aphallic specimens, except that the vas deferens and the penial complex were present.

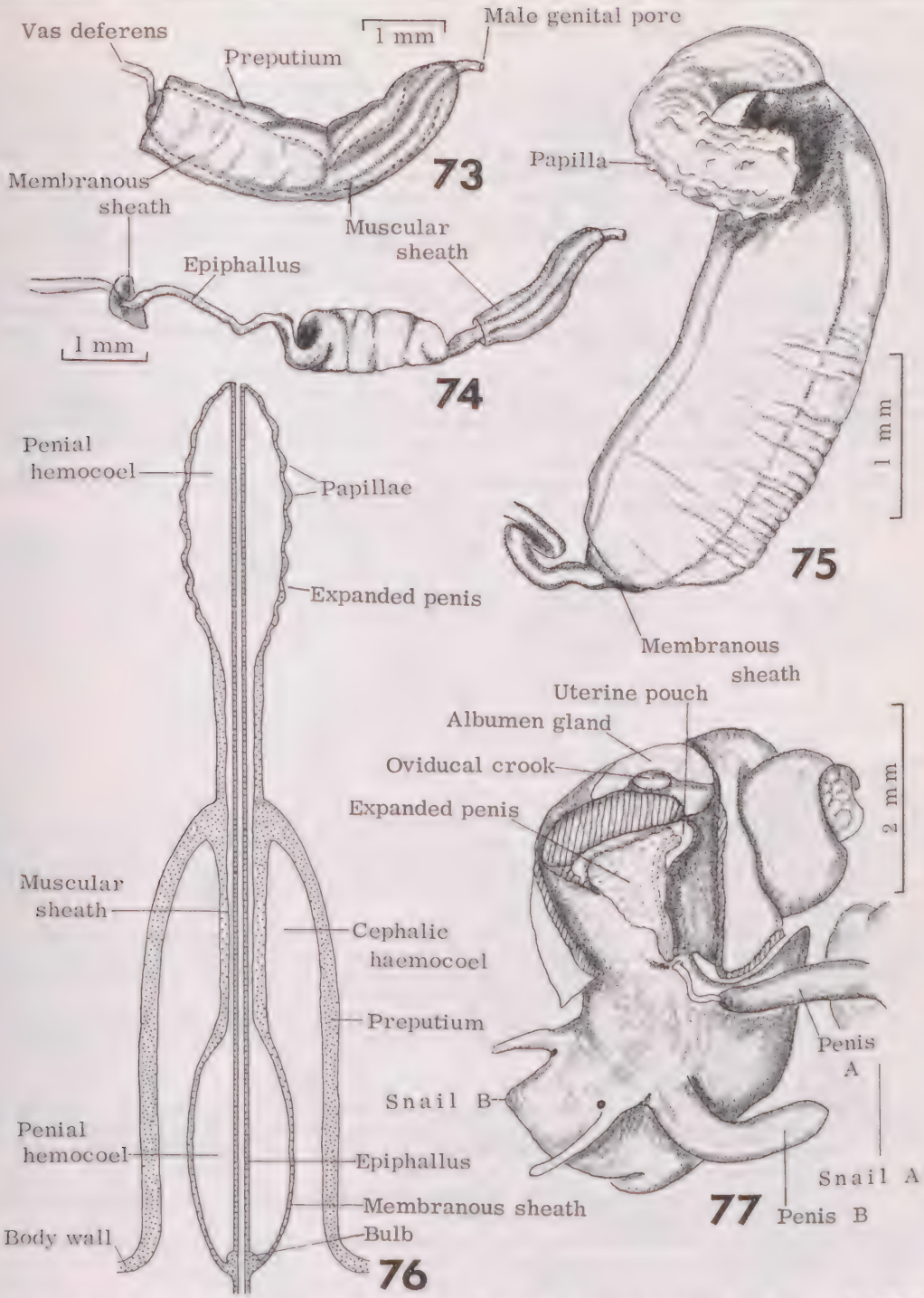
Snails of 6, 7.5 and 9 mm shell length (Figs. 86-90). Aphallic specimens (Figs. 86, 87, 89): The general structure was the same as that described for *Bulinus tropicus* in Section 1, except that the uterine pouches were not seen, the prostate gland was atrophied, and the sperm duct was short and straight.

Euphallic specimens (Figs. 88, 90): The general reproductive structures were as in *Bulinus tropicus*, except that the uterine pouches were not seen.

Relationship of organ sizes (areas, ventral view). The size relationship between the ovotestis and albumen gland during their growth were the same as those found in population I.

Relationships between the sizes of albumen gland (Ag) and prostate gland (P), and spermatheca (Sp) and prostate gland, for 6 size groups, are tabulated as follows:

Shell size group (in mm)	Euphallic		Aphallic	
	Ag : P	Sp : P	Ag : P	Sp : P
3	1 : 1	1 : 3-4	1 : 1	1 : 3-4
4	1 : 1	1 : 6	1 : 1-2	1 : 3-5
5	1 : 0.5-1	1 : 4-8	1 : 2-3	1 : 1-3
6	1 : 1	1 : 5	1 : 5-10	1 : 1
7	-	-	1 : 3	1 : 5
8	1 : 1	1 : 5	1 : 3-5	1 : 1



FIGS. 73–75. Penial complex of *Bulinus tropicus*. 73, The everted penial complex, showing the everted preputium (cut off near junction of body wall) lodging the penial sheath (dotted line) within; 74, Both preputium and membranous part of penial sheath removed to show uncoiled epiphallus (thin part) and penis (thick part); 75, Penial complex with everted, expanded penis, showing the papillae of the luminal lining of the penis on the outside. The preputium has been cut near the junction of the body wall.

FIG. 76. Diagrammatic structure of the penial complex of a bulinine snail, expanded as in Fig. 75. This figure derives from Demian's fig. 29 (1960).

FIG. 77. Copulation of *Bulinus natalensis:* snail A (right; only preputium, expanded penis and part of foot shown) extends its penis into the uterus of snail B (left; dorsal part of uterus and mantle has been removed).

Population III (*Bulinus hexaploidus*, n=54). Figs. 91-95

All 20 specimens dissected were euphallic.

Snails of 3 mm shell length (Figs. 91, a-b). The ovotestis was large compared to the rest of the system. The ovisperm duct was comparatively long and had no seminal vesicle enlargements in its upper half. The primordium of the albumen gland could not be clearly seen. The oviduct-uterus-vagina complex was an undifferentiated tube. Although the spermatheca and prostate gland could be seen, male ducts leading out of the prostate gland were not discerned. No penial complex was seen.

Snails of 4.5 mm shell length (Fig. 92, a-b). The ovotestis was still the largest organ in the system. The ovisperm duct was long and still had no seminal vesicle enlargements in its upper half. The primordium of the albumen gland had appeared. The male system could be clearly recognized. The penial complex had a U-bend at its proximal end.

Snails of 6 mm shell length (Figs. 93, a-b). The reproductive organs had matured as described for population I in Section 1. The ovotestis, however, was still the largest organ, and the albumen gland was extremely small when compared to the ovotestis and prostate gland. The spermatheca was an elongate rod with a club-like terminus.

Snails of 7.5 and 9 mm shell lengths (Figs. 94, a-b, 95, a-c). The general structure was the same as described in Section 1. However, 2 types of specimens were observed, one with a relatively smaller, blackish albumen gland (Fig. 95b) and the other with a larger and whitish to brown albumen gland (Fig. 95c).

Relationship of organ size (area, ventral view). The size relationship between the ovotestis and albumen gland during growth was similar to population I.

Relationships between the sizes of albumen gland (Ag) and prostate gland (P), and spermatheca (Sp) and prostate gland, for 7 shell size groups, are tabulated as follows:

Shell size group (mm)	Ag : P	Sp : P
4	1 : 2-5	1 : 2-5
5	1 : 4-5	1 : 4-5
6	1 : 4	1 : 4-5
7	1 : 5-7	1 : 4-6
8	1 : 5	1 : 5
9	1 : 1.5-2	1 : 3 & 1 : 1
10	1 : 1	1 : 1 & 1 : 1

Population IV (*Bulinus octoploidus*, n=72). Figs. 96-100

All 35 specimens examined were euphallic.

Snails of 3 mm shell length (Figs. 96, a-b). The ovotestis was a sponge-like tissue and had no differentiated follicular structure. The primordium of the albumen gland was observed. Both sperm duct and oviduct were clearly distinguished. The prostate gland appeared square in shape, distinguishing it from the rod-like spermatheca. The uterus-vagina complex was still an undifferentiated tube. The penial complex was slightly curved in its proximal portion.

Snails of 4.5 mm shell length (Figs. 97, a-b). The ovotestis was extremely large and follicular in structure. In the upper half of the ovisperm duct the seminal vesicle enlargement had appeared. The oviducal bend was distinct. The oöthecal and muciparous regions of the uterus had begun to differentiate. No uterine pouches were observed. The penial complex had a U-bend.

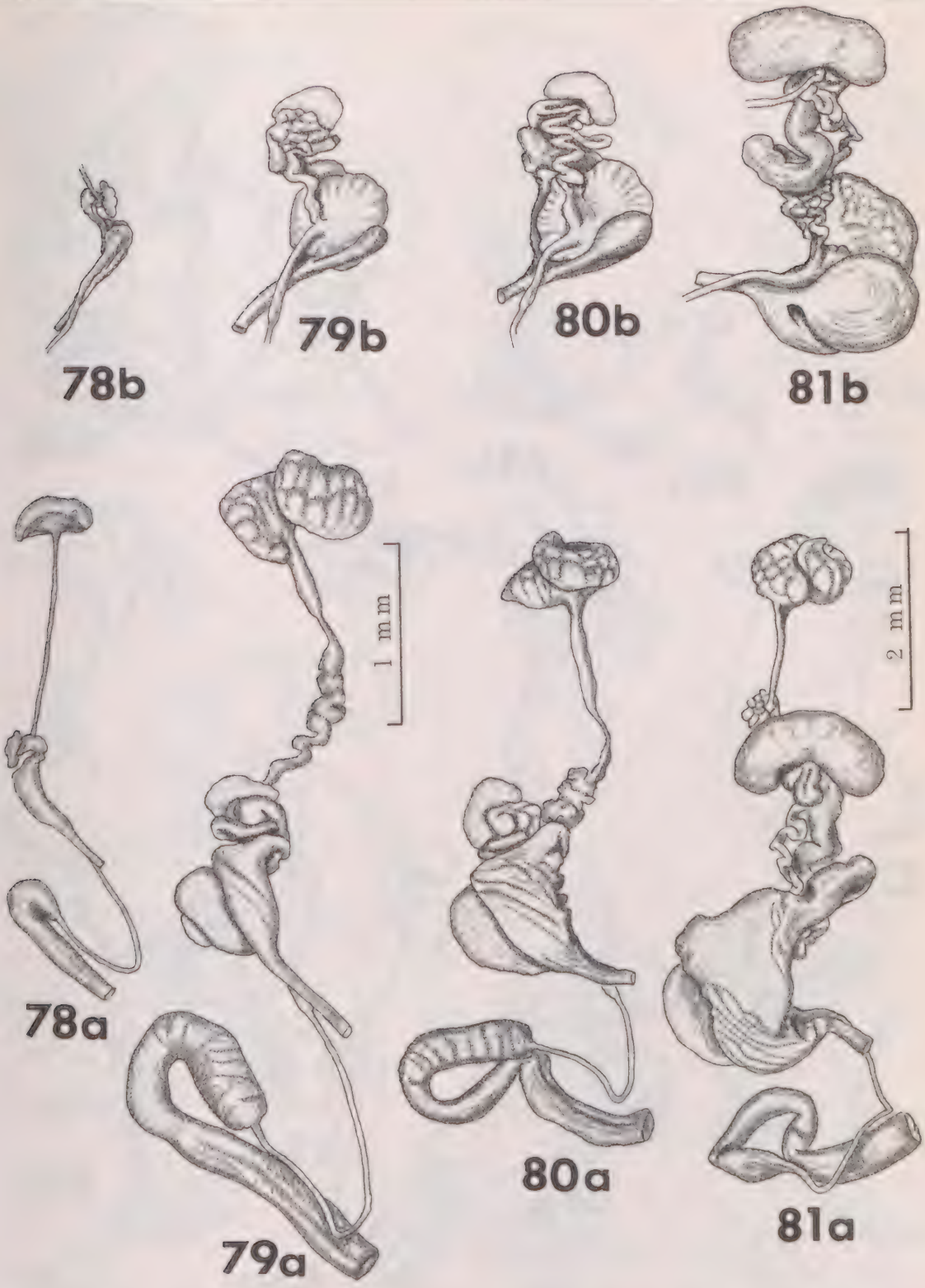
Snails of 6 mm shell length (Figs. 98, a-b). Although the general structure of the reproductive system at that size was identical to that described in Section 1, the ovotestis was still the largest organ in the system. The sperm duct was short and not convoluted.

Snails of 7.5 and 9 mm shell lengths (Figs. 99, a-b; 100, a-b). The general details of structure of the reproductive system are identical to those described in Section 1. The preputium of the penial complex was cordate or pear-shaped, probably due to partial protrusion of the penis into the preputium. This phenomenon consistently appeared in specimens with shells longer than 6 mm, probably because of the relaxation and killing methods used.

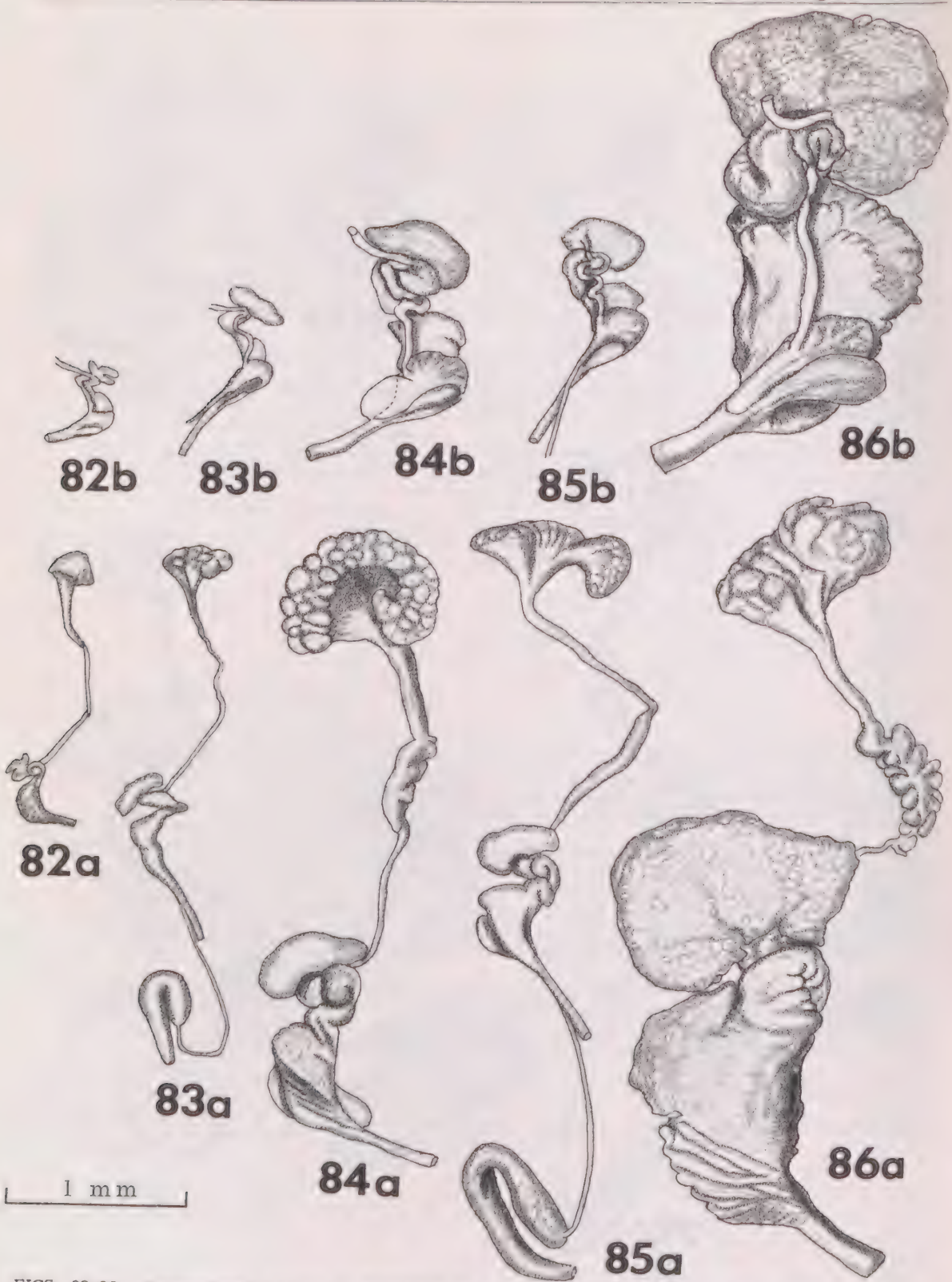
Relationship of organ size (area, ventral view). The size relationship between the ovotestis and albumen gland during growth was the same as that of population I.

Relationships between the sizes of albumen gland (Ag) and prostate gland (P), and spermatheca (Sp) and prostate gland for 8 shell size groups are tabulated as follows:

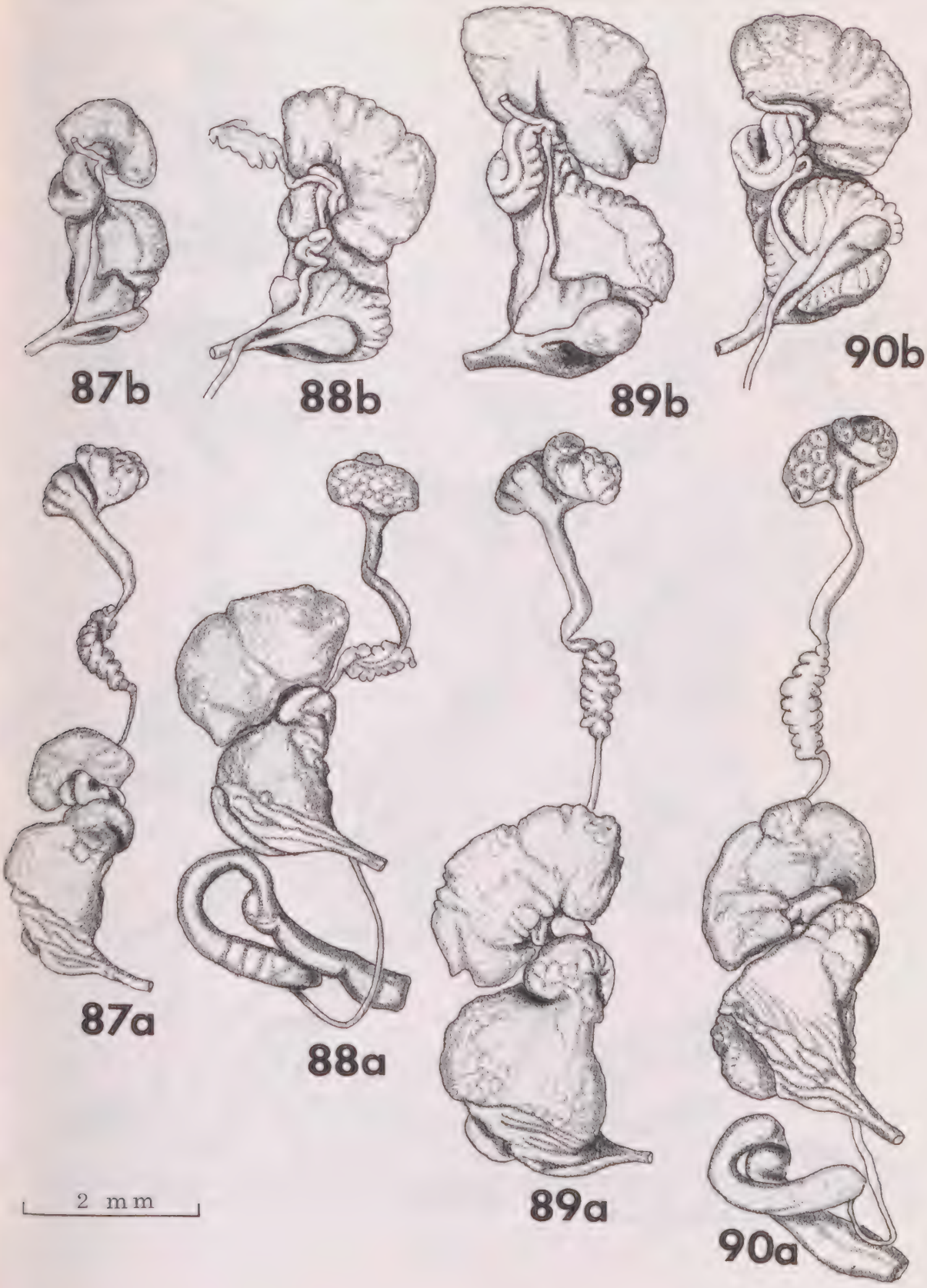
Shell size group (mm)	Ag : P	Sp : P
3	1 : 3	1 : 3
4	1 : 3	1 : 3
5	1 : 2	1 : 5
6	1 : 2	1 : 5
7	1 : 1	1 : 4
8	1 : 1	1 : 4
9	1 : 0.9	1 : 4
10	1 : 0.5	1 : 4

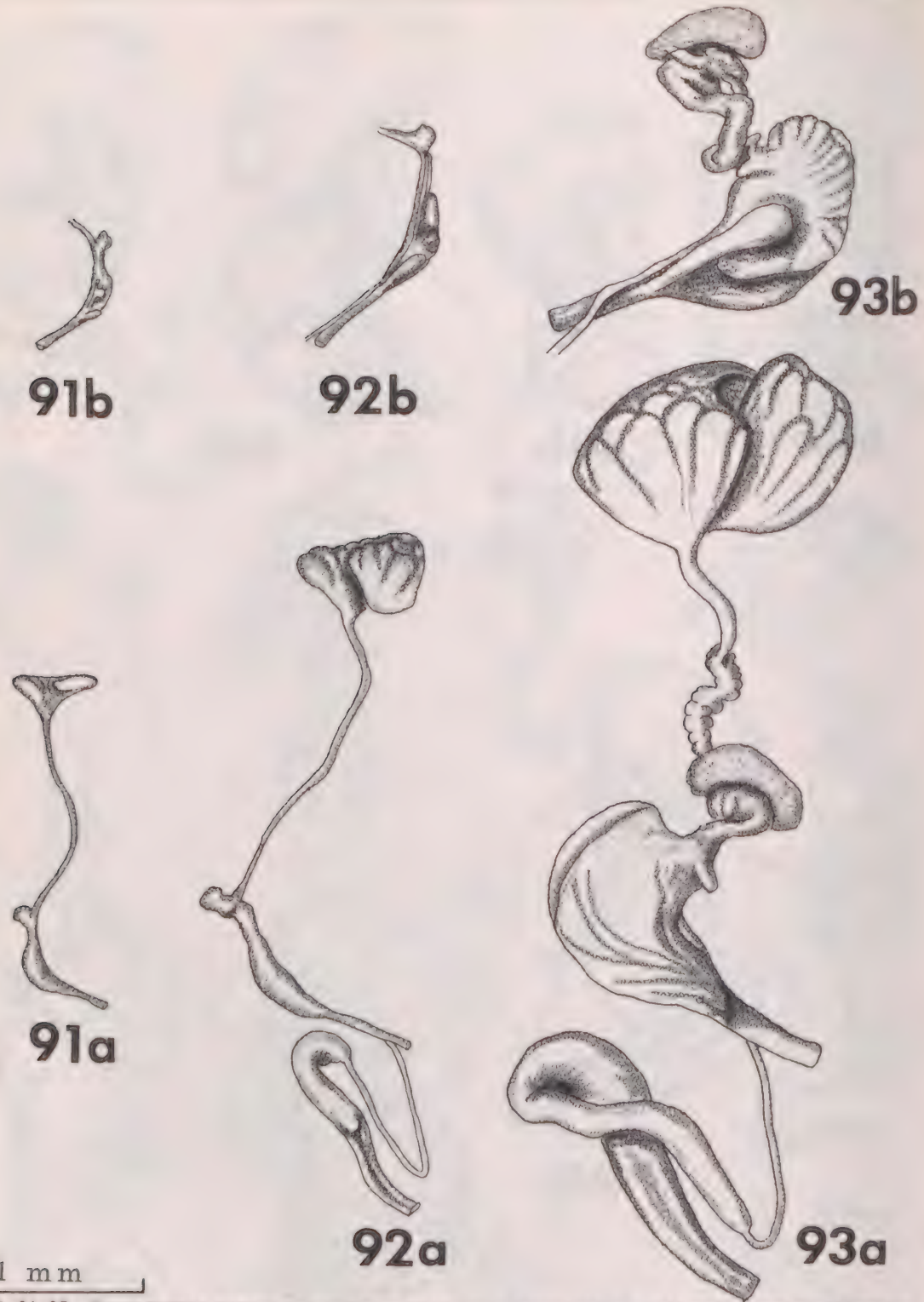


FIGS. 78-81. Reproductive system in population I (*Bulinus tropicus*, n=18) at different shell lengths. 78, 3 mm; 79, 4.5 mm; 80, 6 mm; 81, 7.6 mm. a, dorsal view; b, ventral view. Scale for Figs. 78-79 at Fig. 79a and scale for Figs. 80-81 at Fig. 81a.



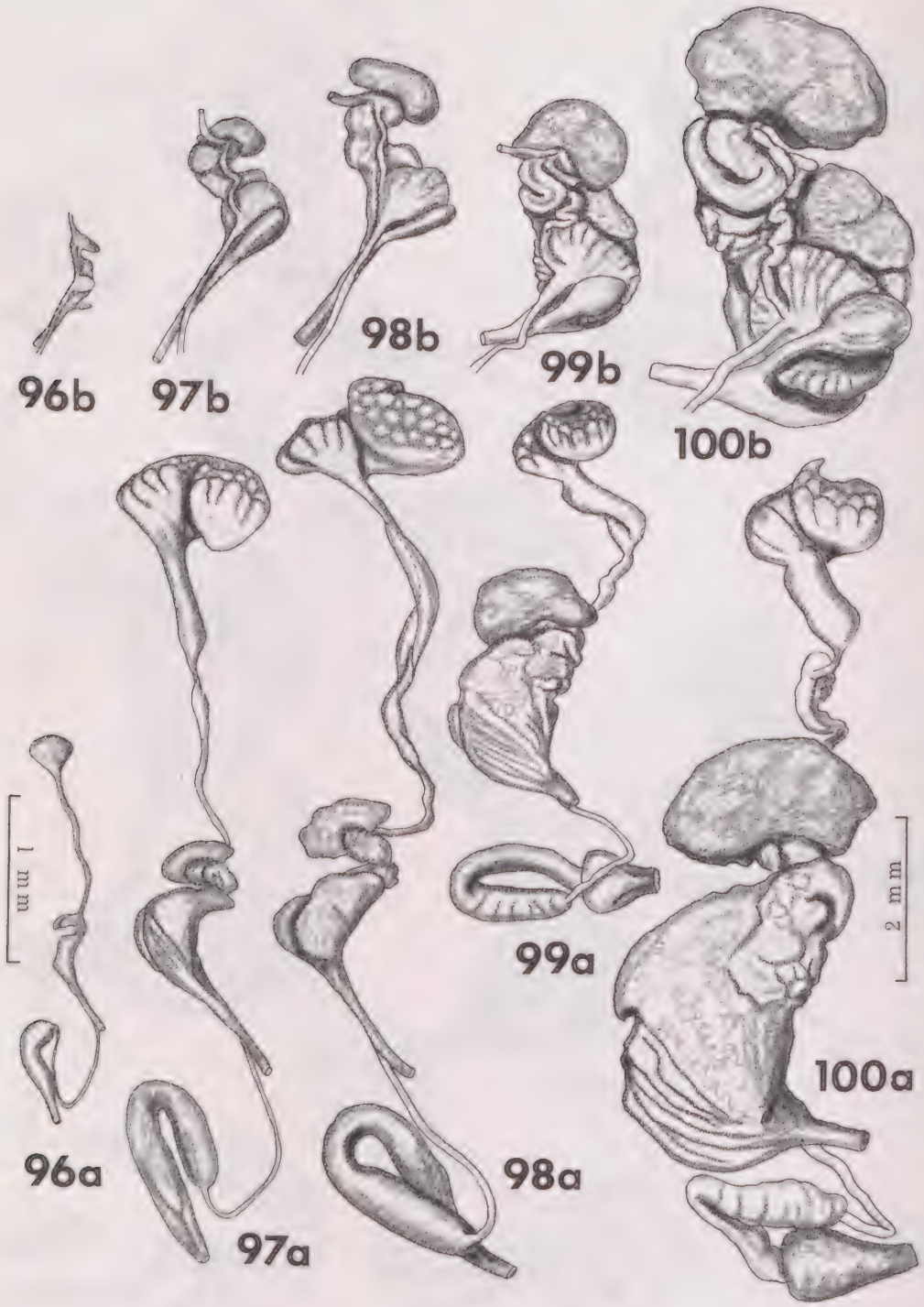
FIGS. 82-90. Reproductive system in population II (*Bulinus truncatus*, n=36) at different shell lengths. 82, Aphallic snail, 3 mm; 83, Euphallic snail, 3.6 mm; 84, Aphallic snail, 4.6 mm; 85, Euphallic snail, 4.3 mm; 86, Aphallic snail, 6 mm; 87, Aphallic snail, 7.5 mm; 88, Euphallic snail, 7.5 mm; 89, Aphallic snail, 8.9 mm; 90, Euphallic snail, 8.9 mm. a, dorsal view; b, ventral view.


87b
88b
89b
90b
87a
88a
89a
90a
2 mm



FIGS. 91-95. Reproductive system in population III (*Bulinus hexaploidus*, n=54) at different shell lengths. 91, 3 mm; 92, 4.5 mm; 93, 6 mm; 94, 7.5 mm; 95, 9 mm. a, dorsal view; b and c, ventral views to show 2 types of albumen gland formation.

95b
95c
94b
95a
2 mm
94a



FIGS. 96-100. Reproductive system in population IV (*Bulinus octoploidus*, n=72) at different shell lengths. 96, 3 mm; 97, 4.5 mm; 98, 6 mm; 99, 7.6 mm; 100, 9.5 mm. a, dorsal view; b, ventral view. Scale for Figs. 96-98 is at Fig. 96a and scale for Figs. 99-100 is at Fig. 100a.

VI. Electrophoresis

Visual inspection and densitometry of stained gels showed that 10 esterase fractions were detectable from populations I, III-VI, VIII and F_1 hybrids from the crosses A, E, O, R and V. A diagrammatic representation of the various fractions with their R_f values is shown in Fig. 101. Two areas in the gels consist of diffuse bands, designated as fractions 1 and 6 in Fig. 101. Fraction 1 (R_f=0.804) is a fast moving component, while fraction 6 (R_f=0.276) is a slow moving one. Subfraction designated 6a (R_f=0.354) is observed in populations III, IV and VIII, and subfraction 6b (R_f=0.208) is found in population V. Fractions 7-10 also appeared sometimes as diffuse components.

The comparison of esterases between adult F_1 hybrids and their parental populations are described in section VII (see p 135, 139, 145, 149 and 151; Figs. 102-106).

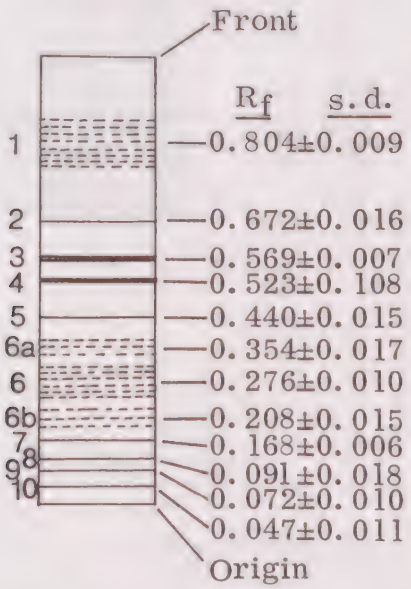


FIG. 101. Diagram of electrophoretically separated foot muscle esterases observed in populations I, III-VI, VIII of *Bulinus*. Mean R_f values and standard deviations (s.d.) are given on the right of the diagram; the numerals identifying the various fractions are on the left. The distance in the gel from origin to front is approximately 35 mm.

VII. Cross-breeding Experiments

1. Albino *Bulinus tropicus* (population V, n=18, Transvaal) x pigmented *B. tropicus* (population I, n=18, Transvaal)

Two consecutive crosses (A, B), each involving a pair of snails to be cross-mated, were conducted.

Cross A, December 1969 to June 1970

The snail with eye-pigment was observed to mate (acting as male) with the albino on 8 December 1969 and the reciprocal mating was observed the next day. Both snails started spawning within 24 hours after mating. For the first 8 weeks, F_1 progeny from this mutual crossing and from both parents were all pigmented. The F_2 progeny descended from brother-sister matings of the F_1 generation were: 1,784 pigmented and 562 albino snails from the pigmented parent and 1,289 pigmented and 415 albino snails from the albino parent (Table 3). The ratio of pigmented to albino snails was roughly 3:1 in either case. Electrophoretically separated foot muscle esterases of pigmented F_1 hybrids from both the albino parent and the pigmented parent of a cross were compared to the electrophoregrams (Fig. 102A), diagrams (Fig. 102B) and densitometric tracings (Fig. 102C) of the parent populations. It is seen that the esterase pattern of the F_1 from each parent (H^I, H^V, Fig. 102 A-C) resembles the albino parent (P^V, Fig. 102 A-C) in that there is a band 6b (R_f=0.208) present, which is absent in the pigmented parent. F_1 hybrids also resemble the pigmented parent (I) in having a weak band 5 (R_f=0.440), which is absent in the albino parent. Furthermore, the optical densities of band 3 (R_f=0.569) in F_1 hybrids nearly equal the sums of those albino and pigmented parents (Fig. 102C). In summary, both parents had mutually cross-fertilized, and eye pigment was inherited in a simple Mendelian fashion. Electrophoretically separated foot muscle esterases of F_1 hybrids showed bands in positions characteristic of both pigmented and albino parents.

Three F_1 descendants from each of the parents were each backcrossed with an albino in order to

TABLE 3. Albino *Bulinus tropicus* (population V, n=18, Transvaal) x pigmented *B. tropicus* (population I, n=18, Transvaal): F_1 and F_2 progenies.

Generation	Cross A				Cross B			
P:	Pigmented		x Albino		Pigmented		x Albino	
Week / F_1:	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino
1st	98	0	62	0	0	0	14	0
2nd	41	0	28	0	11	0	23	0
3rd	55	0	55	0	2	0	43	0
4th					1	0	11	0
5th	86	0	99	0	19	0	3	0
6th	48	0	50	0	13	0	2	0
7th	53	0	18	0	13	0	1	0
8th	39	0	1	0	4	0	NS	
9th	23	0	0	1	NS		NS	
10th	16	0	1	3	2	0	0	1
11th	–	–	0	4	41	0	NS	
12th	16	0	0	6	76	0	NS	
13th	3	0	0	0	44	0	0	27
14th	S-NH		0	24	33	0	0	36
15th	S-NH		0	1	14	0	NS	
16th	NS		NS		13	0	0	2
17th	NS*		NS		8	0	NS	
18th			Discontinued		1	0	NS	
19th					S-A		NS	
20th					NS		Discontinued	
21st					Discontinued			
Totals F_1:	478	0	314	39	295	0	97	66
F_2:	Pigmented 1,784 Albino 562		Pigmented 1,289 Albino 415		All pigmented		Pigmented 511 Albino 146	
Ratio F_2:	3.2 : 1		3.1 : 1				3.5 : 1	

P, parental generation; F_1, first filial generation; F_2, second filial generation obtained by brother-sister mating; NS, no spawn; S-A, spawn with abnormal egg mass; S-NH, spawn but no hatching; *experimental snail died.

further test the ratio of pigmented to albino snails. These backcrosses were as follows: In Backcrosses a, b and c, 10th week offspring from the eye-pigmented parent were used (Table 4). Backcross a: both the eye-pigmented F_1 snail and the albino failed to reproduce. Backcross b: the eye-pigmented F_1 snail produced only eye-pigmented snails (441), and the albino produced pigmented snails (52) in the first 2 weeks, ceased reproduction for 1 week and thereafter produced only albino snails. Backcross c: the eye-pigmented F_1 snail failed to reproduce, but the albino gave issue to 236 eye-pigmented and 12 albinos in the first 5 weeks, which was followed by 1 week of resting. In conclusion, 3 snails failed to reproduce, which may be attributed to some unknown genetic or gametic incompatibility. One snail (eye-pigmented snail of Backcross b) was homozygous in eye-pigment character; therefore, it could not be determined whether cross- or self-fertilization had taken place. One albino snail (Backcross b) was cross-fertilized for only 2 weeks. One albino snail (Backcross c) was cross-fertilized, but it also produced offspring by self-fertilization.

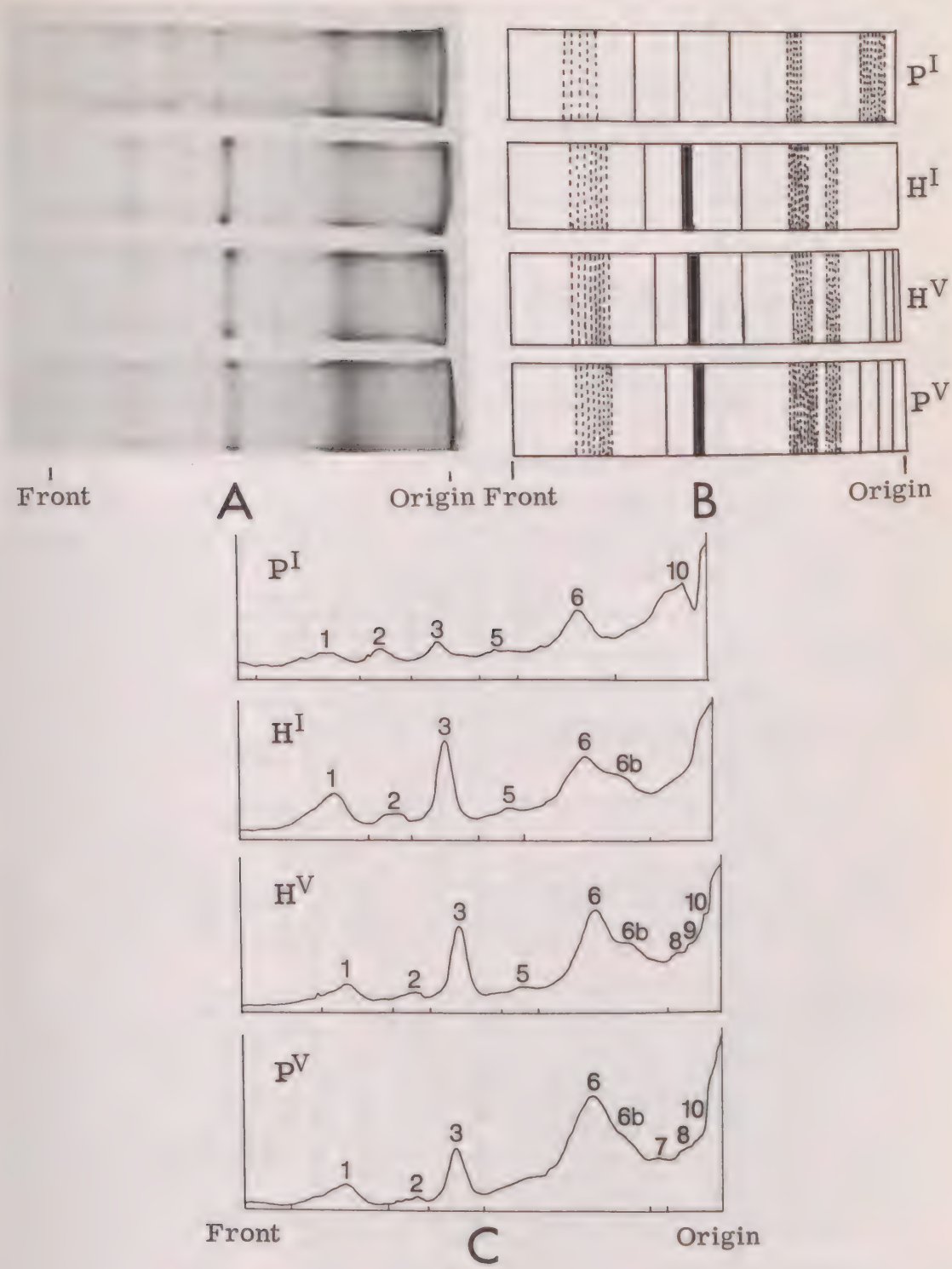


FIG. 102. Electrophoretically separated foot muscle esterases of adult F_1 hybrids (H^I, H^V) and their parents (P^I, P^V) of Cross A. A, photograph; B, diagram; C, densitometric tracing (note: integrator marks on the base line); H^I, F_1 hybrid descended from P^I; H^V, F_1 hybrid descended from P^V; P^I, *Bulinus tropicus* (n=18, Transvaal); P^V, albino *B. tropicus* (n=18, Transvaal).

TABLE 4. Backcrosses of Cross A; progeny obtained by backcrossing 3 pigmented F_1 snails from a pigmented parent with an albino each.

Generation		Backcross a				Backcross b				Backcross c			
P		10th week F_1		x Albino		10th week F_1		x Albino		10th week F_1		x Albino	
Week	Prog.	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino
1st		S-NH		NS		27	0	26	0	NS		42	2
2nd		S-NH		NS		120	0	26	0	NS		81	1
3rd		S-NH		NS		96	0	NS		NS		55	0
4th		S-NH		NS		89	0	0	15	NS		35	8
5th		S-NH		NS		51	0	0	88	NS		23	1
6th		S-NH		NS		58	0	0	42	NS		NS	

TABLE 5. Backcrosses of Cross A; progeny obtained by backcrossing 3 pigmented F_1 snails from an albino parent with an albino each.

Generation		Backcross d				Backcross e				Backcross f			
P		2nd week F_1		x Albino		2nd week F_1		x Albino		2nd week F_1		x Albino	
Week	Prog.	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino
1st		57	46	0	5	39	31			50	59	58	16
2nd		29	26	0	6	26	20	13	16	23	39	29	29
3rd		12	13	NS		8	4	28	27	35	24	40	27
4th		37	17	0	5	13	3	26	50	29	35	4	8
5th		103	29	0	12	27	12	5	1	9	9	NS	
6th		58	13	Discontinued		37	10	NS		22	9	S-NH	
Total		296	144	0	28	150	80	72	74	168	177	131	120
Ratio		2.1 : 1		-		1.9 : 1		1 : 1		1 : 1		1 : 1	

Prog., progeny; P, parental generation; NS, no spawn; S-NH, spawn but no hatching.

In the second series of Backcrosses d, e, and f, 3 second week F_1 snails obtained from the albino parent were each mated to an albino (Table 5). Backcross d: the eye-pigmented F_1 snails produced 296 eye-pigmented and 144 albino snails in 6 weeks, roughly in a ratio of 2 : 1. The albino produced only albinos during 5 weeks indicating selfing, for which reason this experiment was discontinued. Backcross e: the eye-pigmented F_1 snail produced 150 eye-pigmented and 80 albino snails in 6 weeks, in roughly a 2 : 1 ratio. The albino snail produced 72 pigmented and 74 albino snails in 5 weeks and then rested for 1 week. The ratio was 1 : 1, as expected. Backcross f: the pigmented F_1 snail produced 168 pigmented and 177 albino snails in 6 weeks, in roughly a 1 : 1 ratio. The albino snail produced 131 eye-pigmented and 120 albino snails in the first 4 weeks, in roughly a 1 : 1 ratio, as expected. However, in the 5th week it rested and in the 6th week it reproduced abnormal, non-embryonated egg masses. In conclusion, 3 snails gave the expected ratio, one snail reproduced by self-fertilization, and 2 snails gave a 2 : 1 ratio.

Cross B, 12 August 1970 to 30 November 1970

The eye-pigmented snail used was observed to mate (acting as male) with the albino on 4 and 7 September. The 1st egg mass was observed on 8 September. The F_1 progeny from both parents all had eye-pigment. The F_2 progeny from the sibling matings of the F_1 generation descended from the eye-pigmented parent were all eye-pigemented, which indicated that the pigmented parent had been self-fertilizing. The F_2 progeny descended from the albino parent consisted of 511 eye-pigmented and 146 albino snails, which was roughly in a ratio of 3 : 1, as expected (Table 3). In summary, the eye-pigmented parent had self-fertilized, while the albino parent had been cross-fertilized; the eye-pigment character was inherited in a simple Mendelian fashion.

2. Albino *Bulinus tropicus* (population V, n=18, Transvaal) x pigmented *B. natalensis* (population VI, n=18, Natal)

Three tests (C, D, E,) were made during the period from 4 March 1971 to 21 September 1971. Additionally, the offspring of the cross-fertilized parent were observed for shell characters so as to determine the pattern of inheritance of shell color and spire length. The albino *Bulinus tropicus* used came from a population having a brown shell and medium high spire (L/AL = 1.36), while the eye-pigmented *B. natalensis* used characteristically had a white, low-spired shell (L/AL = 1.27).

Cross C. The 1st egg mass was observed on 29 March and the snails were subsequently isolated. The eye-pigmented parent did not oviposit for 4 weeks but reproduced 43 eye-pigmented young beginning the 5th week. The albino parent produced 78 eye-pigmented snails in the first 5 weeks and died during the 6th week (Table 6). The F_2 progeny descended from the sibling mating of the F_1 progeny from the eye-pigmented parent were all eye-pigmented; those from the albino parent consisted of 183 eye-pigmented and 39 albino snails (Table 6). Of 15 surviving F_1 generation snails from the albino parent, 13 had medium-spired and 2 had low-spired shells; 12 shells were brown and 3 white; and, in 23 surviving F_2 generation snails, there were 19 individuals with medium and 4 with low-spired shells; 17 shells were brown and 6 white (Table 7).

Cross D. The albino (acting as male) was observed to mate with the eye-pigmented snail on 5 April. The 1st egg mass was observed on 9 April. The eye-pigmented snail did not spawn for the first 5 weeks and then laid abnormal, non-embryonated egg masses for the next 2 weeks and died. The albino parent produced 134 pigmented F_1 snails in the first 6 weeks and died during the 7th week. The F_2 progeny descended from sibling matings among the F_1 progeny consisted of 114 eye-pigmented and 34 albino snails, roughly a 3 : 1 ratio as expected (Table 6). Among 10 surviving F_1 descendents from the albino parent, 9 had medium and 1 had low-spired shells; all 10 shells were brown. Of the 21 observed F_2 generation snails, 1 had high, 6 had medium and 14 had low-spired shells; of these 17 were brown and 4 white (Table 7).

Cross E. The eye-pigmented snail (acting as a male) was observed to mate with the albino on 5 April, and the 1st egg mass was observed on 9 April, at which time the snails were isolated. The eye-pigmented parent did not oviposit during the first 3 weeks but produced 111 eye-pigmented snails from the 4th week on. The F_2 progeny from these latter snails were all eye-pigmented. The albino parent produced 221 pigmented F_1 progeny during the first 11 weeks but stopped egg-laying from the 12th week on. The F_2 progeny from the sibling mating of the F_1 progeny were 142 eye-pigmented and 41 albino snails, roughly a 3 : 1 ratio (Table 6). All of the 22 surviving F_1 descendants of the albino parent observed had medium-spired shells. Of these, 15 were brown and 7 white. Of 20 surviving F_2 generation snails that reached a suitable size, 15 had medium and 5 low-spired shells; 15 had brown and 5 white shells (Table 7). The electrophoretically separated foot muscle esterases of F_1 hybrids (H^V, Fig. 103 A-C) formed an intermediate pattern between both albino and pigmented parents (P^V, P^{VI}, Fig. 103 A-C) by having the bands 3 (R_f=0.569) and 8 (R_f=0.09) resemble the pigmented parent, while the bands 6 (R_f=0.276) and 6b (R_f=0.208) resemble the albino parent. However, the optical density of band 6b of hybrids was much larger than that of the albino parent (H^V, P^V, Fig. 103C).

In summary, the above 3 crosses produced similar results in that (1) the eye-pigmented parent was self-fertilizing after a period of non-spawning (4, 5 and 3 weeks in Crosses C, D and E, respectively), which presumably was due to the incompatibility of the *Bulinus natalensis* genome with that of the albino *B. tropicus*, and (2) pigmented *B. natalensis* had cross-fertilized the albino parent. The eye-pigment character was inherited according to the Mendelian law as 2 alleles on the same locus of the chromosome. Spire height and shell color characters were segregated both in the F_1 and F_2 progeny, but in variable ratios. The electrophoretically separated foot muscle esterases of F_1 snails in Cross E (H^V, Fig. 103) showed banding characters of both parents (P^V, P^{VI}; Fig. 103), which further supports the fact that the pig-

TABLE 6. Albino *Bulinus tropicus* (population V, n=18, Transvaal) x pigmented *B. natalensis* (population VI, n=18, Natal): F_1 and F_2 progenies.

Generation		Cross C				Cross D				Cross E			
P:		Pigmented		x Albino		Pigmented		x Albino		Pigmented		x Albino	
Week	F_1:	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino
1st		NS		11	0	NS		24	0	NS		20	0
2nd		NS		7	0	NS		15	0	NS		36	0
3rd		NS		35	0	NS		42	0	NS		37	0
4th		NS		10	0	NS		27	0	7	0	48	0
5th		12	0	7	0	NS		24	0	11	0	22	0
6th		11	0	NS*		S-NH		2	0	17	0	20	0
7th		2	0			S-NH*		NS*		55	0	18	0
8th		S-NH								15	0	12	0
9th		14	0							2	0	6	0
10th		1	0							4	0	1	0
11th		3	0							Discontinued		1	0
12th		NS										S-NH	
13th		NS*										NS	
14th												NS	
15th												NS	
16th												NS	
17th												Discontinued	
Total	F_1:	43	0	78	0	0	0	134	0	111	0	221	0
Total	F_2:	All pigmented	0	Pigmented 183 Albino 39	0	0	0	Pigmented 114 Albino 34	0	All pigmented	0	Pigmented 142 Albino 41	0
Ratio	F_2	-	-	4.7 : 1	-	-	-	3.3 : 1	-	-	-	3.4 : 1	-

P, parental generation; F_1, first filial generation; F_2, second filial generation obtained by sibling matings; NS, no spawn; S-NH, spawn but no hatching; *experimental snail died.

TABLE 7. Albino *Bulinus tropicus* (population V, n=18) x *B. natalensis* (population VI, n=18). Nature of F_1 and F_2 offspring descended from 3 albino parents used in 3 cross-breeding experiments.*

Generation	Character	Cross C	Cross D	Cross E
P	1. Eye-pigment	(Pig.) Alb.	(Pig.) Alb.	(Pig.) Alb.
	2. Spire height	(L) M	(L) M	(L) M
	3. Shell color	(W) B	(W) B	(W) B
F_1	1. Eye-pigment	Pig. 78 Alb. 0	Pig. 134 Alb. 0	Pig. 221 Alb. 0
	2. Spire height	M 13 L 2	M 9 L 1	M 22 L 0
	3. Shell color	B 12 W 3	B 10 W 0	B 15 W 7
F_2	1. Eye-pigment	Pig. 183 Alb. 39	Pig. 114 Alb. 34	Pig. 142 Alb. 41
	2. Spire height	M 19 L 4	H 1 M 6 L 14	M 15 L 5
	3. Shell color	B 17 W 6	B 17 W 4	B 15 W 5

P, parental generation; F_1, first filial generation; F_2, second filial generation by sibling matings; Pig., pigmented; Alb., albino; H, high with L/AL above 1.51; M, medium with L/AL 1.31-1.50; L, low with L/AL below 1.30; B, brown; W, white.

*The characters of the mate (pigmented *B. natalensis* with low spire and white shell) are given in parenthesis.

mented snail had cross-fertilized the albino one.

3. Albino *Bulinus tropicus* (population V, n=18, Transvaal) x pigmented *B. tropicus* (population VII, n=18, Ethiopia)

Four crosses were carried out during the period from 19 April to August 1971.

Cross F. The albino (acting as male) was observed to mate with the eye-pigmented snail on 27 May. Neither snail laid any eggs. In summary, gametic incompatibility (postmating isolating mechanism) seemed to prevent both snails from reproducing.

Cross G. The 1st egg mass was observed on 6 June and the snails were isolated. The eye-pigmented snail did not spawn and died in the 4th week. The albino snail produced 75 eye-pigmented F_1 progeny in the first 4 weeks and stopped laying from the 5th week on. The F_2 progeny from the sibling mating of the F_1 progeny were 17 eye-pigmented and 14 albino snails in the ratio of 1.2 : 1 (Table 8); 17 embryos died before identification, i.e., embryo mortality was 36%. In summary, the Ethiopian eye-pigmented *Bulinus tropicus* failed to reproduce, probably due to a postmating gametic incompatibility of its ova with South African albino *B. tropicus* sperm. But the Ethiopian pigmented snail did cross-fertilize the albino snail.

Cross H. The 1st egg mass was observed on 29 May. The snails were kept together; they laid abnormal, non-embryonated egg masses continually until both individuals died on 21-25 July. In summary, no progeny was obtained; probably a postmating isolating mechanism, such as gametic incompatibility, or other unknown mechanisms prevented the inclusion of eggs in the egg capsules.

Cross I. The 1st egg mass was observed on 31 May, after which the snails were isolated. The eye-pigmented individual did not oviposit during the first 6 weeks and then laid only abnormal, non-embryonated eggs from the 7th week on. The albino snail produced 26 pigmented F_1 offspring in the 2nd and 3rd weeks, then laid abnormal, non-embryonated eggs for the next 2 weeks, stopped laying for 2 weeks and then died. The F_2 progeny from the sibling mating of the F_1 progeny were 64 eye-pigmented and 23 albino snails, in approximately a 3 : 1 ratio, and 9 embryos died, i.e., there was 9.4% embryo mortality, before identification (Table 8). In summary, the eye-pigmented snail failed to reproduce, but it cross-fertilized the albino parent. The eye-pigment character was inherited in simple Mendelian fashion.

4. Albino *Bulinus tropicus* (population V, n=18, Transvaal) x pigmented *B. truncatus* (population II, n=36, Egypt)

Four Crosses (J, K, L, M) were made during the period 4 August 1970 to 1 April 1971.

TABLE 8. Albino *Bulinus tropicus* (population V, n=18, Transvaal) x pigmented *B. tropicus* (population VII, n=18, Ethiopia): F_1 and F_2 progenies.

Generation		Cross G				Cross I			
P:		Pigmented		x Albino		Pigmented		x Albino	
Week	F_1:	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino
1st		NS		56	0	NS		S-NH	
2nd		NS		13	0	NS		12	0
3rd		NS		5	0	NS		25	0
4th		NS*		1	0	NS		S-NH	
5th				NS		NS		S-NH	
6th				NS		NS		NS	
7th				NS		S-NH		NS*	
8th				NS*		S-NH			
9th						S-NH			
10th						S-NH			
11th						S-NH			
12th						NS*			
Totals	F_1:	0	0	75	0	0	0	26	0
Totals	F_2:			Pigmented 17 Albino 14 (Embryo mortality 17)				Pigmented 64 Albino 23 (Embryo mortality 9)	
Ratio	F_2:			1.2 : 1				2.8 : 1	

P, parental generation; F_1, first filial generation; F_2, second filial generation by sibling matings; NS, no spawn; S-NH, spawn but no hatching; *experimental snail died.

Cross J. The cross started on 4 August 1970 with the 1st egg mass being observed on 30 August. The eye-pigmented snail gave rise to eye-pigmented F_1 progeny, and the sibling mating among these produced all eye-pigmented F_2 progeny. The albino snail failed to spawn during the first 6 weeks, in the 7th it spawned sterile spawn and in the 8th it died (Table 9). In summary, neither snail was cross-fertilized. There was probably some genetic or gametic incompatibility between the 2 mates.

Cross K. The cross started on 4 August 1970 and the 1st egg mass was observed on 30 August. The eye-pigmented snail produced only eye-pigmented F_1 progeny for 28 weeks and then died. The sibling mating among the F_1 progeny also produced only pigmented F_2 progeny. The albino snail failed to spawn for the first 4 weeks and then produced only albino progeny from the 5th week on (Table 9).

Cross L. The cross started on 4 August 1970 and the 1st egg mass was observed on 30 August. The eye-pigmented parent produced eye-pigmented F_1 progeny, and the sibling mating among F_1 progeny also produced only eye-pigmented F_2 progeny. The albino failed to spawn in the first 5 weeks after which the experiment was discontinued (Table 9).

Cross M. The cross started on 4 August 1970, and the albino snail (acting as a male) mated with the eye-pigmented snail on 4 September 1970. The 1st egg mass was observed on 20 September. The eye-pigmented snail produced 35 eye-pigmented young in the first 2 weeks and then died. The sibling mating among the F_1 progeny produced only eye-pigmented F_2 offspring. The albino laid abnormal egg masses for 2 weeks and then died (Table 9).

In summary, the above 4 tests all produced similar results in that neither snail was cross-fertilized, presumably as a result of gametic incompatibility between the 2 mates.

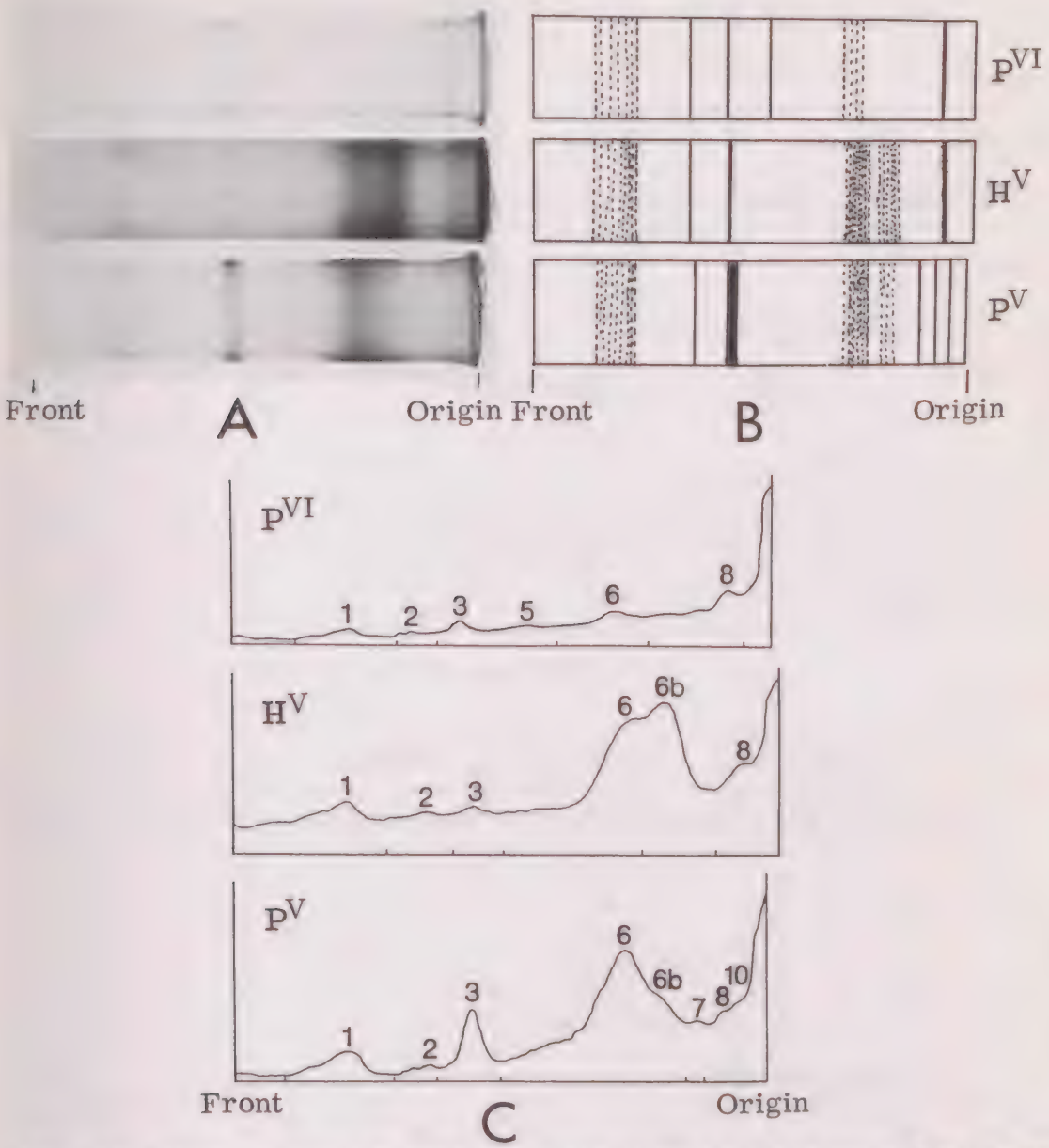


FIG. 103. Electrophoretically separated foot muscle esterases of adult F_1 hybrid (H^V) and its parents (P^{VI}, P^V) of Cross E. A, photograph; B, diagram; C, densitometric tracing (note: integrator marks on the base line); H^V, F_1 hybrid descended from P^V; P^{VI}, *Bulinus natalensis* (n=18, Natal); P^V, albino *B. tropicus* (n=18, Transvaal).

5. Albino *Bulinus tropicus* (population V, n=18, Transvaal) x pigmented *B. sericinus* (population VIII, n=36, Ethiopia)

Three crosses (N, O, P) were made during the period 4 August 1970 to 9 June 1971.

Cross N. The cross began on 4 August 1970. The eye-pigmented parent was observed to mate (acting as male) with the albino parent on 4 September. The 1st egg mass was observed on 8 September and the snails were isolated. Both eye-pigmented and albino parents failed to lay egg masses for 10 and 8 weeks respectively and then died. In summary, no progeny was obtained. Some unknown genetic mechanism prevented these from producing eggs.

Cross O (Table 10). The cross started on 4 August 1970. The albino was observed to mate (acting as

TABLE 9. Albino *Bulinus tropicus* (population V, n=18, Transvaal) x pigmented *B. truncatus* (population II, n=36, Egypt): F_1 and F_2 progenies.

Generation		Cross J				Cross K			
P:		Pigmented		x Albino		Pigmented		x Albino	
Week	F_1:	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino
1st		11	0	NS		4	0	NS	
2nd		14	0	NS		12	0	NS	
3rd		29	0	NS		34	0	NS	
4th		33	0	NS		28	0	NS	
5th		9	0	NS		49	0	0	7
6th		2	0	NS		21	0	0	4
7th		7	0	S-NH		47	0	Discontinued	
8th		NS*		NS*		⋮ Continued			
Totals	F_1:	105	0	0	0	1,073**	0	0	11
	F_2:	All pigmented				All pigmented			

Generation		Cross L				Cross M			
P:		Pigmented		x Albino		Pigmented		x Albino	
Week	F_1:	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino
1st		3	0	NS		5	0	NS	
2nd		15	0	NS		28	0	S-A	
3rd		18	0	NS		2	0	S-A	
4th		21	0	NS		NS*		NS*	
5th		15	0	NS					
6th		9	0	Discontinued					
7th		3	0						
8th		Discontinued							
Totals	F1:	84+	0	0	0	35	0	0	0
	F_2:	All pigmented				All pigmented			

P, parental generation; F_1, first filial generation; F_2, second filial generation obtained by sibling mating; NS, no spawn; S-A, spawn with abnormal egg mass; S-NH, spawn but no hatching; *experimental snail died.

**The sum of F_1 progeny up to the 28th week.

male) with the eye-pigmented parent on 19 and 24 August. The albino never reproduced. The 1st egg mass was observed on 8 September from the eye-pigmented parent, which produced 19 eye-pigmented F_1 progeny in the first 3 weeks and then died. These offspring were maintained for 5 months and proved to be sterile when siblings mated.

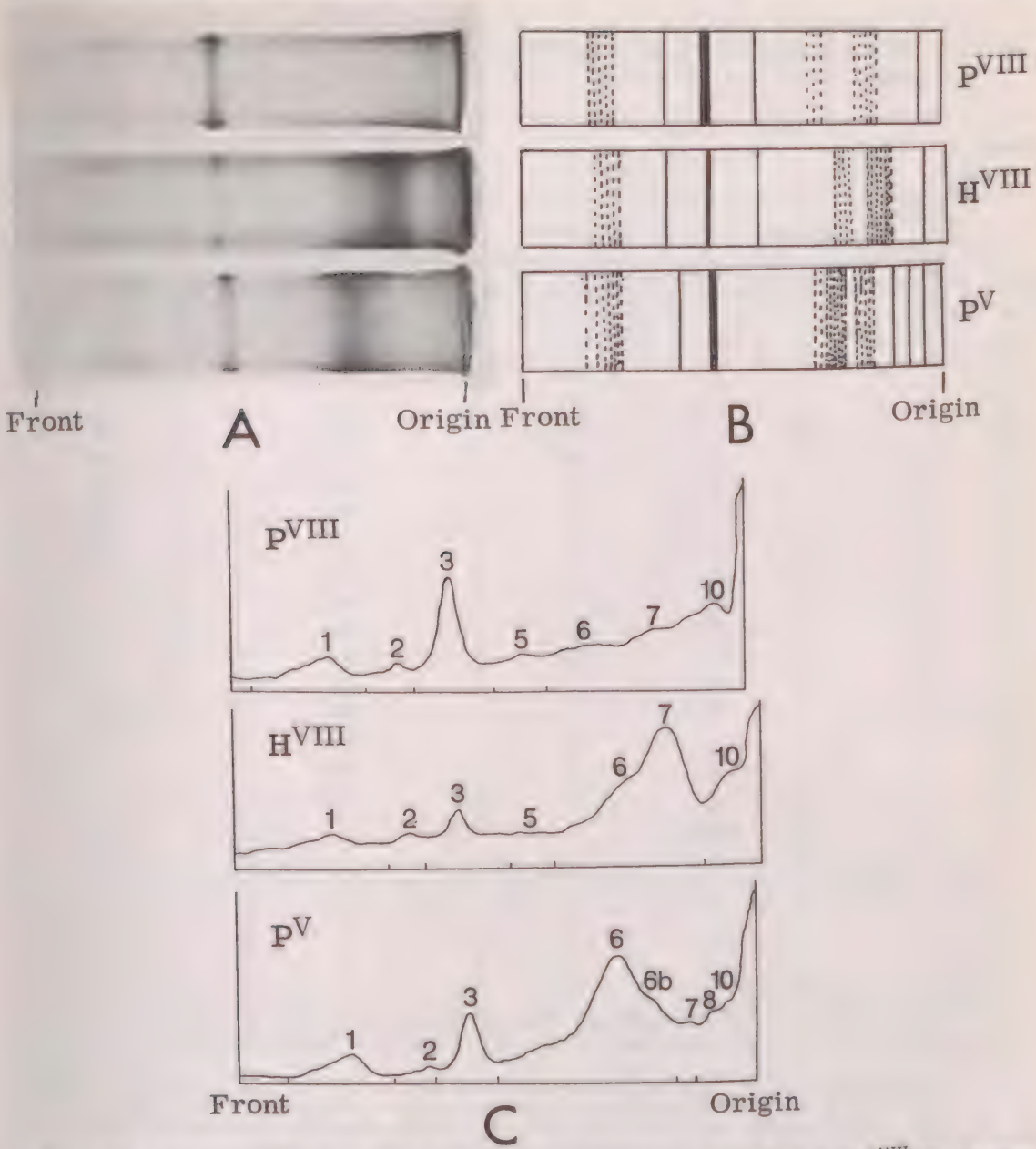


FIG. 104. Electrophoretically separated foot muscle esterases of adult F_1 hybrid (H^{VIII}) and its parents (P^{VIII}, P^V) of Cross O. A, photograph; B, diagram; C, densitometric tracing (note: integrator marks on the base line); H^{VIII}, F_1 hybrid descended from P^{VIII}; P^{VIII}, *Bulinus sericinus* (n=36, Ethiopia); P^V, albino *B. tropicus* (n=18, Transvaal).

The sterile F_1 generation was eye-pigmented and had darkish pigment patches along the mantle edges, similar to their eye-pigmented parent. A study of the gross anatomy of the reproductive system showed that the snails were euphallic and normal, except that the seminal vesicle enlargements were weakly developed. The electrophoretically separated foot muscle esterases of F_1 hybrids (Fig. 104) from the pigmented parent had the smaller optical densities of fraction 3 (R_f=0.569), intermediate densities of fraction 6 (R_f=0.276), and fraction 7 (R_f=0.168) had larger optical densities than those of both parents (Fig. 104C).

After 5 1/2 months, "sterile" F_1 snails were backcrossed to albinos. The results of 2 such crosses (a, b) were as follows:

Backcross a. On 16 March 1971, an eye-pigmented, "sterile" snail with a 6.3 mm shell (184 days old) was mated with an albino snail with a 5.8 mm shell. The 1st egg mass was observed on 29 March and the

TABLE 10. Albino *Bulinus tropicus* (population V, n=18, Transvaal) x pigmented *B. sericinus* (population VIII, n=36, Ethiopia): F_1 and F_2 progenies.

Generation	Cross O				Cross P			
P:	Pigmented		x Albino		Pigmented		x Albino	
Week / F_1:	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino
1st	4	0	NS		NS		0	2
2nd	6	0	NS		NS		0	1
3rd	9	0	NS		NS		0	7
4th	NS*		NS		NS		NS	
5th			NS*		NS		NS	
6th					NS		NS	
7th					NS		NS	
8th					NS		NS	
9th					NS		0	6
10th					NS		0	58
11th					NS		0	79
12th					NS		0	21
13th					NS		0	16
14th					NS		S-A	
15th					NS		S-A	
16th					NS		0	3
17th					NS*		0	9
18th							S-A	
19th							NS*	
Totals F_1:	19	0	0	0	0	0	0	192
Totals F_2:	0							

P, parental generation; F_1, first filial generation; F_2, second filial generation by sibling matings; NS, no spawn; S-A, spawn with abnormal egg mass; *experimental animal died.

snails were separated. The eye-pigmented snail produced 38 eggs, 22 embryos developed abnormally, and none of them hatched. One abnormality in eye-pigmented embryos concerned the shell which expanded like that of a limpet; normal shells were also observed in albino embryos from the same parent. The albino parent was self-fertilizing and the experiment was discontinued on 1 April.

Backcross b. The starting date was 16 March 1971. The 2 parents were an eye-pigmented, "sterile" snail with a 6.4 mm shell (177 days old) and an albino snail with a 6.4 mm shell. The 1st egg mass was observed on 29 March and the snails were separated. The eye-pigmented snail laid 519 eggs, 118 developed, and only 7 snails (3 eye-pigmented, 4 albino) survived to hatching stage. Of these, 1 eye-pigmented snail grew to adulthood and then laid 1 egg mass on 31 July 1971, but no embryos developed. The same abnormalities as in Backcross a were observed in the embryos. The albino parent laid no egg masses for 3 weeks and died on 19 April.

In summary, the albino parent failed to reproduce, but it had cross-fertilized *Bulinus sericinus*. The F_1 progeny, which was sterile upon sibling mating, abortively reproduced when backcrossed to the albino.

Cross P (Table 10). The experiment started on 4 August 1970. The albino parent was observed to mate (acting as male) with the eye-pigmented snail on 21 August and 3 September. The 1st egg mass from the albino snail was observed on 12 October. The eye-pigmented snail laid no egg masses in 17 weeks and then died. The albino parent produced 10 albino snails (with 50% mortality) in the first 3 weeks, rested for 5 weeks, resumed reproduction of albino progeny without any embryo mortality for 10 weeks, after which it died.

In summary, neither snail had cross-fertilized the other. A postmating isolating mechanism such as gametic incompatibility prevented these snails from producing F_1 progeny.

TABLE 11. Albino *Bulinus tropicus* (population V, n=18, Transvaal) x pigmented *B. hexaploidus* (population III, n=54, Ethiopia): F_1 and F_2 progenies.

Generation	Cross Q				Cross R			
P:	Pigmented		x Albino		Pigmented		x Albino	
Week / F_1:	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino
1st	45	0	NS		22	0	NS	
2nd	39	0	NS		22	0	NS	
3rd	56	0	Discontinued		10	0	Discontinued	
4th	19	0			1	0		
5th	40	0			S-A			
6th	22	0			S-A			
7th	51	0			S-A			
8th	17	0			NS			
9th	13	0			NS			
10th	Discontinued				NS			
11th					Discontinued			
Totals F_1:	302+	0	0	0	55	0	0	0
Totals F_2:	0	-	-	-	0	-	-	-

Generation	Cross S				Cross T			
P:	Pigmented		x Albino		Pigmented		x Albino	
Week / F_1:	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino	Pigmented	Albino
1st	8	0	NS		NS		0	30+
2nd	21	0	0	10+	10	0	0	30+
3rd	24	0	0	10+	44	0	0	20+
4th	28	0	Discontinued		24	0	0	10+
5th	48	0			61	0	Discontinued	
6th	19	0			26	0		
7th	11	0			39	0		
8th	NS	0			19	0		
9th	NS				36	0		
10th	NS				31	0		
11th	Discontinued				5	0		
12th					14	0		
13th					5	0		
14th					Discontinued			
Totals F_1:	159	0	0	20+	314	0	0	90+
Totals F_2:	0	-	-	-	0	-	-	-

P, parental generation; F_1, first filial generation; F_2, second filial generation by sibling matings; NS, no spawn; S-A, spawn with abnormal egg masses.

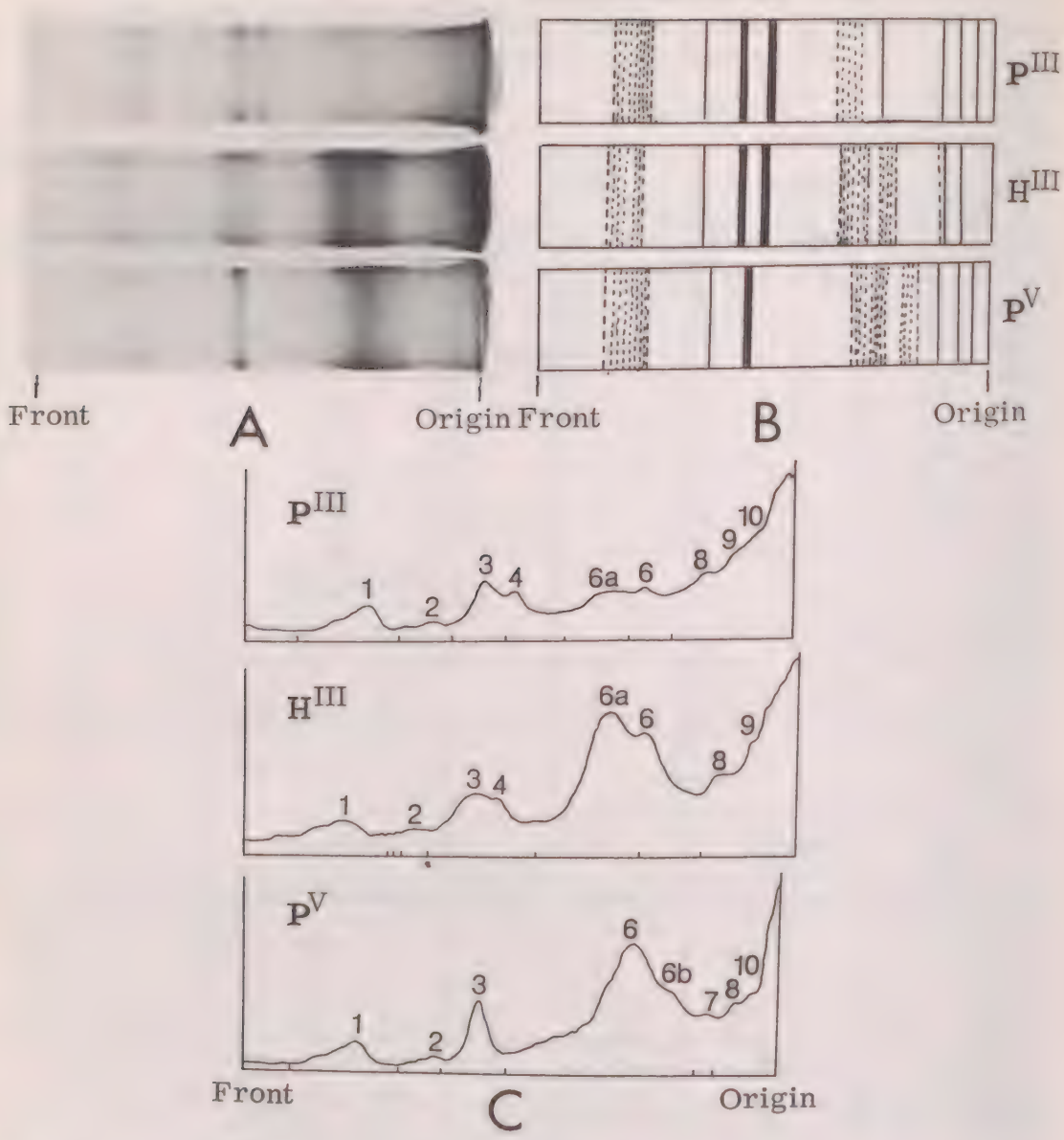


FIG. 105. Electrophoretically separated foot muscle esterases of adult F_1 hybrid (H^{III}) and its parents (P^{III}, P^V) of Cross R. A, photograph; B, diagram; C, densitometric tracing (note: integrator marks on the base line); H^{III}, F_1 hybrid descended from P^{III}; P^{III}, *Bulinus hexaploidus* (n=54, Ethiopia); P^V, albino *B. tropicus* (n=18, Transvaal).

6. Albino *Bulinus tropicus* (population V, n=18, Transvaal) x pigmented *Bulinus hexaploidus* (population III, n=54, Ethiopia)

Four crosses (Q, R, S, T, Table 11) were made during the period 21 December 1969 to May 1971.

Cross Q. The cross started on 21 December 1969. The albino snail (acting as male) was observed to mate with the eye-pigmented parent on 6, 19 and 20 January 1970. The 1st egg mass was observed on 20 January from the eye-pigmented parent, which produced 302 eggs in 9 weeks. All F_1 progeny were healthy eye-pigmented snails, though they were sterile, i.e., there was no progeny from sibling mating. The albino snail laid no egg masses for 2 weeks, and the experiment was discontinued.

Cross R. The cross started on 8 January 1970. The albino (acting as male) was observed to mate with the eye-pigmented parent on 19, 23 and 26 January. The 1st egg mass from the eye-pigmented snail was observed on 1 February. The snail produced 55 eggs in 4 weeks, laid abnormal masses for the next 3

TABLE 12. Albino *Bulinus tropicus* (population V, n=18, Transvaal) x pigmented *B. octoploidus* (population IV, n=72, Ethiopia). Cross W: F_1 progeny of the pigmented parent.

Generation		Cross W		Fertility
P		Pigmented		Fertile
Week	F_1	Pigmented	Albino	
1st		12	0	
2nd		17	0	
3rd		23	0	
4th		20	0	
5th		14	0	
6th		22	0	Sterile
7th		17	0	
8th		NS		
9th		NS		
10th		7	0	
11th		NS		
12th		NS		
13th		NS		
14th		13	0	
15th		12	0	Fertile
16th		NS		
17th		6	0	

P, parental generation; F_1, first filial generation; NS, no spawn.

weeks and then did not lay eggs until the experiment was discontinued. All eggs hatched and the snails were healthy, but they failed to produce a new generation. The albino snail laid no egg masses for 2 weeks and was not observed thereafter.

Cross S. Observations started on 8 January 1970. The albino snail (acting as male) was seen to mate with the eye-pigmented snail on 10 January. The 1st egg mass was observed on 15 January. The eye-pigmented parent produced 159 eggs in 7 weeks and then laid no eggs for the next 3 weeks, after which the experiment was discontinued. The eggs hatched into healthy snails with eye-pigment. The sibling matings, however, produced no viable progeny, although egg masses were laid in which all the embryos developed up to the blastula stage. The albino parent laid no egg masses during the 1st week but produced albino progeny from the 2nd week on.

Cross T. The experiment started on 12 January 1970. The albino parent (acting as male) was observed immediately to mate with the eye-pigmented parent, which displayed its penis continually on 12-13 January. The 1st egg mass was observed on 15 January. The eye-pigmented parent did not spawn during the 1st week but laid 314 eggs in the next 12 weeks before the experiment was discontinued. All of the embryos hatched and were healthy eye-pigmented snails. No F_2 progeny were obtained from sibling mating by the F_1 progeny. The albino parent laid only albino progeny for 4 weeks, at which time the experiment was discontinued.

In summary, the above 4 experiments all produced closely similar results in that the eye-pigmented parents all produced eye-pigmented, vigorous F_1 progeny, which were sterile when mated to one another. The electrophoretically separated foot muscle esterases of F_1 hybrids (H^{III}, Fig. 105 A-C) from the pigmented parent were similar to those of the pigmented parent in having the fractions 4 (R_f=0.523) and 6a (R_f=0.354), which were absent in the albino parent (P^{III}, P^{V}, Fig. 105 A-C). The optical density of fraction 6 (R_f=0.276) of the F_1 hybrid (H^{III}, Fig. 105C) was about the same as that of the albino parent (P^{V}, Fig. 105C) and larger than that of the pigmented parent (P^{III}, Fig. 105C). The albino parents always acted as the male partner during copulation but were not cross-fertilized: 2 failed to reproduce, while 2 self-fertilized and produced albino offspring.

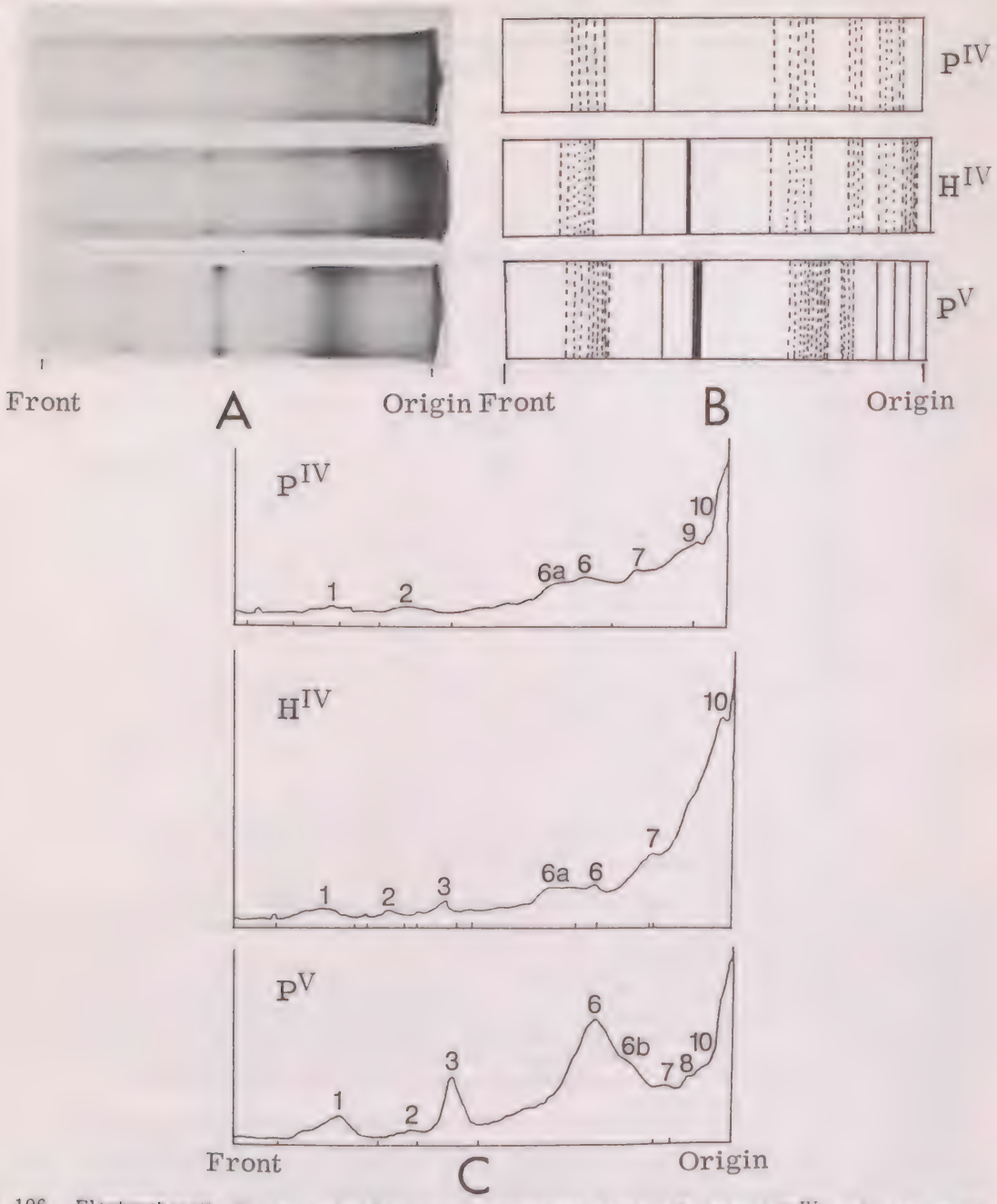


FIG. 106. Electrophoretically separated foot muscle esterases of adult F_1 hybrid (H^{IV}) and its parents (P^{IV}, P^{V}) of Cross V. A, photograph; B, diagram; C, densitometric tracing (note: integrator marks on the base line); H^{IV}, F_1 hybrid descended from P^{IV}; P^{IV}, *Bulinus octoploidus* (n=72, Ethiopia); P^{V}, albino *B. tropicus* (n=18, Transvaal).

7. Albino *Bulinus tropicus* (population V, n=18, Transvaal) x pigmented *Bulinus octoploidus* (population IV, n=72, Ethiopia)

Four crosses (U, V, W, X) were made during the period 27 October 1970 to June 1971.

Cross U. The test started on 27 October 1970. The albino snail (acting as male) was observed to mate with the pigmented snail on 22 and 26 November 1970 and 15 January 1971. The albino died on 30 January. The eye-pigmented parent laid an abnormal egg mass on 5 February 1971, i.e., 21 days after the last mating. It died on 1 March. Both snails failed to produce progeny.

Cross V. The experiment started on 27 October 1970. The eye-pigmented snail died on 3 December. The albino parent laid its 1st egg mass on 22 January 1971, which was 50 days after its eye-pigmented

mate died. The albino produced 39 albino snails and then alternated reproductive and non-reproductive periods for 11 weeks, when the experiment was discontinued.

Cross W. The experiment started on 27 October 1970. The eye-pigmented snail died on 11 November 1970 and was replaced by another snail of equivalent size (5 mm). The albino parent (acting as male) was observed to mate with the 2nd eye-pigmented snail on 26 November 1970. The 2nd mate also died, on 2 December, and was replaced by a 3rd snail of 8 mm shell length. The albino parent (acting as male) was observed to mate with the 3rd eye-pigmented snail on 4, 6 and 27 December. The 1st egg mass was observed on 28 December and the snails were separated. The 3rd eye-pigmented snail produced eggs for 7 weeks, then alternated reproductive and non-reproductive periods and finally died. The albino snail failed to oviposit and died. The reproductive activities of the pigmented parent are summarized in Table 12.

The sterile F_1 snails produced during the first 10 weeks by the eye-pigmented parent were the result of cross-fertilization with the albino snail, whereas the fertile snails reproduced after the 14th week were the result of self-fertilization. The eggs laid by the sterile progeny were not embryonated. Histological studies revealed that no sperm were produced in the ovotesticular tubules of the F_1 snails (Figs. 64, 66) and that there were only 0-2 ova in the distal part of the tubules (Fig. 62) instead of 5-6, as in normal snails (Fig. 61). The electrophoretically separated foot muscle esterases of these sterile snails (H^{IV}, Fig. 106 A-C) were similar to those of the albino parent (P^{V}, Fig. 106 A-C) in having a fraction 3 (R_f=0.569) and also similar to the pigmented parent (P^{IV}, Fig. 106 A-C) in having a fraction 6a (R_f=0.354). Thus, it seems that the foot muscle esterases of F_1 hybrids showed banding characters of both parents.

Backcrosses of sterile snails to an albino were unsuccessful.

Cross X. The experiment started on 27 October 1970. The eye-pigmented snail died on 11 November and was replaced by another of equivalent size (4.4 mm). The 2nd snail died on 3 December 1970 and was replaced by a 3rd snail of equivalent size which died on 25 December 1970. After isolation for 3 months, the albino parent started laying abnormal egg masses from 1 April 1971 to 19 April and died on 3 May 1971.

In summary, the above 4 crosses gave similar negative results. The albino snail was observed to act as the male partner during copulation. It was never successfully cross-fertilized, the only viable young being obtained by self-fertilization. The pigmented snail gave no spawn or abnormal spawn, except in one case, where sterile offspring were produced in Cross W. Mortality among eye-pigmented Ethiopian octoploids was high. It is suspected that the repeated early death of the pigmented mate may have been due to mechanical injury caused at mating by the albino partner.

DISCUSSION

I. Shell Morphology

Systematics within the "subgenus" *Bulinus* remained obscure due to the lack of sufficient knowledge about (1) the ontogenetic change in shell characters, (2) the extent of character variability in the species, (3) which are of genetic and which of environmental origin, and (4) which characters are useful for taxonomy.

The outlines of typical shells of the 4 populations studied here are presented in Figs. 5-8. They ranged from 3 to 9 mm in length. The basic shell outlines within the same population are, in general, the same, except that there is a change in certain mathematical ratios, such as L/AL (shell length to aperture length, indicating spire length), which can be attributed to growth changes. The increase of L/AL with L (Table 1, Fig. 9) indicates that small shells are more depressed than large shells. The same growth changes in shell forms have been observed also in *Bulinus jousseaumei* (Wright, 1957).

The microsculpture of the shell also changes ontogenetically. The embryonic shell has punctae regularly arranged (Walter, 1962, 1968), and the first whorl of the postembryonic shell always has regularly spaced ribs, which gradually decrease in prominence from the second whorl on. In some shells, prominent ribs persist up to the body whorl. This might be an example of heterochrony but, more probably, is due to 2 alleles (smooth vs. ribbed) on the same locus on a chromosome.

The difficulties in interpreting past classical descriptions of shell features lie in the fact that the limits of character variability were neither recognized nor clearly defined, while shell characters for any one species often overlap and merge with those found in other species. For this reason public health workers have tended to oversimplify by lumping the multiplicity of species. Amberson & Schwartz (1953), for example, united 81 names under one nominal species,

Bulinus truncatus. To properly define species, it is necessary to determine which characters are significant.

Qualitative characters, such as shape of shell, aperture and spire; profile of whorl and suture; sculpture; thickness and color of shell, may be useful within the "subgenus" if accompanied by certain accurate measurements. Quantitative data regarding size of shell, aperture, height of spire, number of whorls, can be useful if the age or size composition of the samples are known. Characters such as broadness of callus, shape of columella and presence of the umbilicus, are not important because: (1) These are frequently uniform in laboratory-bred specimens (Figs. 5, 6, 8), and (2) if not, then all degrees of differences may occur in a population due to age and physiological differences of the snails. Brown, *et al.* (1971) stated that in the *tropicus-natalensis* complex the umbilicus, like the columella, was highly variable within population samples, all 4 of the categories he distinguished being represented in 48 samples. In some samples the umbilicus was closed in small shells and open in large ones, but in others the umbilicus was open or closed over the whole size range.

Brown, *et al.* further found that populations with different mean values for spire length (L/AL) were correlated with a geographical pattern, and also that there was a significant difference in spire length between 2 samples collected at different times from the same locality, when different ecological conditions prevailed. These findings suggested that spire length was an ecophenotypic character. In the present study, the height of the spire was demonstrated to be a definable genetic character, since medium and low spire characters segregated in both F_1 and F_2 progeny of cross-mated parents (Table 7).

Another pair of shell characters such as brown vs. white color was also demonstrated to have a genetic basis in that brown and white shells segregated in both F_1 and F_2 progeny of cross-mated parents.

Although the genetic origin of the above 2 pairs of shell characters (medium spire vs. low; brown shell vs. white) was apparent, the mode of inheritance was not in a simple Mendelian fashion. The segregation of these characters in both F_1 and F_2 generations suggested that they are polygenic. Similar shell characters (clear color vs. amber; high vs. low) in *Biomphalaria glabrata* were also suggested to be genetically determined (Richards, 1970).

The ratio L/AL gives an indication of the exsertion of the spire. If the spire is strongly depressed, the ratio will approach unity, while it will increase with the exsertion of the upper whorl. This ratio has been used by Wright (1957, 1965), Brown (1966) and Brown, *et al.* (1971). In this study, the height of the spire is also expressed in terms of L/AL, applying the term "low" for values below 1.30, "medium" for 1.31-1.50, "high" for 1.51-1.70 and "extremely high" for 1.71 and above.

The ratio L/AW (shell length to aperture width) expresses the relationship between the increase in diameter of the body whorl with increasing shell length. Corresponding results are obtained by using the ratio shell length/shell diameter (L/W) (Wright, 1957). This latter ratio might provide a good index for shell form. For example, in populations I and III L/W is 1.51 and 1.58, respectively, and represents narrow forms, while in populations II and IV, L/W is 1.44 and 1.38, respectively, representing more globose forms.

The ratio AL/AW (aperture length to aperture width) gives an indication of the shape of the aperture, for, if it is round, the ratio will approach unity, whereas the ratio will increase as the aperture narrows. If AL/AW is near 1.5, the aperture is oval, ovate, or obovate (depending on whether the broadest part is near the center, the lower half, or the upper half). If AL/AW approaches, or

is larger than 2.0, the aperture is oblong (round at both ends), elliptic, lanceolate, or oblanceolate (depending on whether the broadest part is at the center, the lower half, or the upper half).

The ratios L/AL and L/W (Table 1, Figs. 9, 10) showed only a slight increase with shell length in all 4 populations. The means for the ratios AL/AW appeared to lie within more or less fixed limits, with ranges of 1.67-1.93 for population I, 1.62-1.85 for II, 1.94-2.11 for III and 1.67-1.81 for IV.

The mean values of L/AL showed that populations I and II were high-spired with values of 1.54 and 1.53 respectively, while populations III and IV were medium-spired with values of 1.42 and 1.39.

The comparisons of L/W (shell length to width) values (Fig. 10) showed that they were practically always higher for populations I and III than for populations II and IV, indicating that the latter is more globose in shell form. This globosity is also reflected in the aperture form; populations II and IV had smaller values of AL/AW than populations I and III (Fig. 11). Population III had the highest value of AL/AW and possessed the narrowest aperture.

There was a strong correlation between the shell length and width (Fig. 12). Comparison of the widths showed that populations II and IV have higher values than population I and III, indicating that in the former the outline of the body whorl was more rounded than in the latter.

In summary, populations I and II are high-spired, while populations III and IV are medium-spired. However, judged from the shapes of the body whorl and aperture, populations II and IV are similar, i.e., they are more globose than populations I and III, the latter 2 being more slender.

II. Pigmentation of Animals

The head and foot region of live bulinine snails is of different shades of reddish-brown or buff, the red component being due to hemoglobin in the blood and the remainder to pigmentation. Albinos are pale to bright red because the hemoglobin is not masked by surface pigmentation. The presence of a yellow-green coloration in the head region over the velar margin, the superior tentacle lobe, "rhinophoral" groove and foot margin indicates the presence of yellow or green pigments in addition to the black pigments. However, there are as yet no studies on the nature of these pigments in bulinine snails.

Mandahl-Barth (1958) described the animals of the *tropicus* group as dark-colored, strongly pigmented, and those of the *truncatus* group as whitish or grayish, usually with black spots on the mantle, although darker animals are not uncommon. A survey of mantle markings described for the *truncatus* group reveals considerable variation: *Bulinus rohlfsi* varies from unmarked to strongly patterned (Wright, 1963b, 1965); *B. sericinus* is black patterned at different intensities (Wright, 1965; Wright & Brown, 1962); the mantle pattern of *B. truncatus* is black and that of *B. guernei* is intensely black (Wright, 1956). The present study, based on laboratory-bred specimens, showed that *B. truncatus* (Fig. 14, a-c) and *B. octoploidus* (n=72)(Fig. 16, a-c) were pale gray without any mantle markings, while *B. tropicus* (Fig. 13, a-c) showed a strong black pattern and *B. hexaploidus* (n=54) (Fig. 15, a-c) was dark gray with a weak pattern of black pigment. This similarity between populations II and IV and between populations I and III may possibly reflect their closer relationships.

A survey of black pigmentation on the tunica propria overlying the visceral hump also revealed considerable variation. Demian (1960) reported it to be unpigmented and transparent in *Bulinus truncatus*. The present study, based on laboratory-bred

specimens, also showed that the tunica propria of *B. truncatus* (n=36) (population II) was completely lacking in black pigmentation. *B. sericinus* (n=36) from its type locality (Toquor River at Mekerka) has no pigmentation, but some specimens have light pigmentation on the area overlying the ovotestis[6]. *B. tropicus* (population I) and *B. octoploidus* (n=72, population IV) had no pigmentation except for the area overlying the ovotestis, and *B. hexaploidus* (n=54, population III) had an evenly and deeply black pigmentation. These observations demonstrate that there is no parallel relationship between the pigmentation of the tunica propria and that of the mantle among the 4 populations studied.

According to the literature the *africanus* group has a black-pigmented mantle as reported for *Bulinus africanus* (Brown, 1965), *B. globosus* (Wright, 1963b), *B. jousseaumei* (Wright, 1956, 1957), *B. ugandae* (Brown, 1965), and *B. angolensis* (Wright, 1963b). Similar reports exist for the *forskalii* group, for *B. camerunensis* (Wright, 1965), *B. reticulatus* (Wright, 1963a), *B. beccari* (Wright, 1963a), *B. scalaris* (Wright, 1963b), *B. forskalii* (Wright, 1956, 1963b), *B. crystallinus* (Wright, 1963b) and *B. ludovicianus* (Wright, 1956).

Thus the normal diploid *tropicus*, *forskalii* and *africanus* groups all have strongly pigmented mantles, while in the *truncatus* group, where polyploidy has evolved, this feature varies from unpigmented in *Bulinus truncatus* to pigmented in *B. sericinus*.

White flecks are present on the foot and in the head regions of *Bulinus* (Stiglingh, *et al.*, 1962), as well as in other Planorbidae (Baker, 1945). The origin, nature and physiological significance of these white flecks are not known, nor has the possible systematic significance of their distribution patterns been given any attention in the past. *B. truncatus* (population II) has aggregated patches of flecks over the area anterior and medial to the eyes (Fig. 17), a pattern which differs from that in the other 3 populations where the flecks are more evenly scattered. Although the white flecks were observed to increase with age, there were differences of intensity in the different populations. Richards (1969), who demonstrated that mantle pigmentation was an inherited character in *Biomphalaria glabrata*, further suggested (1970) that the white granules in the head and tentacles were also inherited characters, in which case they might constitute a useful taxonomic character.

III. Radulae

As pointed out by Baker (1945), if the planorbid radula is to be used as a taxonomic character, then the age and degree of wear of the teeth should be considered, which, in turn, depends on its place on the radular ribbon (see Figs. 25-27). However, only a few workers have indicated that position for the teeth they depicted. Among these is Schutte (1965, 1966), who described the radulae from 20-30 transverse rows of *Bulinus*. Baker (1945) was not only concerned with the location of the tooth, but also with its tilt, i.e., with the natural position of the radula on the radular ribbon. In practice, this ideal cannot be attained, since the preparation process may, and does, tilt and rotate the teeth in any direction. However, since the orientation of the "natural position on the radular ribbon" was not defined, the author arbitrarily assigned the orientation defined as "D"

[6]Wright & Brown (1962) reported the epithelium overlying the visceral hump of "*Bulinus sericinus*" to be evenly and deeply pigmented. However, it is not known to which species group their specimens belonged.

(Fig. 20D) as the standard position. It is here proposed that the right half of the 30th (= 5) transverse row from the anterior end, together with the rachidian tooth, all with a "D" orientation, should be given in future radular work for the purpose of radular comparison, provided that all the lateral teeth have the same orientation as their corresponding rachidian neighbor.

Recent studies concerning the radulae of *Bulinus tropicus* are those of Stiglingh, *et al.* (1962) on populations from the Transvaal and Cape Province, South Africa; Wright (1965) on material from west Cameroon; Schutte (1965) on snails from Transvaal, the Cape, Swaziland and Kenya; and Brown *et al.* (1967) on *Bulinus* from Transvaal, Natal and Cape provinces, South Africa. The present study agrees with the account of Brown, *et al.* (1967) in that the 1st lateral tooth had smoothly curved triangular mesocones and small triangular endocones. It disagrees with that of Stiglingh, *et al.* (1962), whose material was described as having a *"truncatus* type" radula (see next paragraph) but was in fact similar to the intermediate or *natalensis* group, as described by Brown, *et al.* (1967), i.e., the mesocone of 1st lateral tooth has one side smoothly curved and the other side angulated. The account of Wright (1965, p 89, fig. 12) seems to relate to radular teeth from the posterior portion of the radula, which might not offer a sound basis for comparison.

Recent studies on the radula of *Bulinus truncatus* are those of Demian (1960) on Egyptian populations, Brown, *et al.* (1967) on snails from Egypt and Iran and Walter (1968) on Egyptian material. These reports and the present study uniformly found an angular-sided mesocone and an expanded endocone on several innermost lateral teeth.

The radulae of *Bulinus hexaploidus* and *B. octoploidus* were similar to that of the "intermediate" type (Brown, *et al.*, 1967) with respect to the mesocone. Furthermore, the splitting of the endocone in these 2 populations occurred nearer to the rachidian tooth, and the lateral edge of the hook-body was more pronouncedly serrated than that in *B. tropicus* and *B. truncatus*.

The radula of *Bulinus hexaploidus* (population III, n=54) was similar to that of *B. tropicus* (population I, n=18) in that the L1 and L2 teeth have a small and short endocone and ectocone. The radula of *B. octoploidus* (population IV, n=72) was similar to that of *B. truncatus* (population II, n=36) in that the lateral teeth had an expanded endocone and a small, triangular ectocone.

The most distinctive features noted in our strains were deformities in the teeth. Whereas our *Bulinus tropicus* (population I) always had normal teeth, the *B. truncatus* (population II) showed a characteristic rachidian deformity, *B. hexaploidus* (population III) had lateral teeth with missing endocones and *B. octoploidus* (population IV) showed fusion of several innermost lateral teeth.

Tooth deformities have been reported in *Biomphalaria pfeifferi* (Schutte & Van Eeden, 1959) and in *Bulinus truncatus* (El-Gindy & Rushdi, 1962; Brown, 1965). Once a deformity occurs, it occurs throughout the longitudinal row concerned. It could well be due to a genetic factor, and the different deformities may reflect differences in the genetic constituents of the populations.

We thus have 4 cytologically distinct and geographically separated populations which could be distinguished on the basis of many radular characters, such as the shape of cusps, splitting of the endocone, appearance of denticles between the cones and of serrated edges of the hook-body, and even by the frequency and type of tooth deformity.

In order to study the variability of radulae between different populations, or within or between different species or species groups, various workers have undertaken biometrical studies (Berrie, 1959; Schutte, 1965; van Aardt & Van

Eeden, 1969). Unfortunately, they choose unreliable elements, such as length of cusp, to calculate their ratios, i.e., B/E[7] (Berrie, 1959) and b/a[8] (Schutte, 1965). From Berrie's description, the cusp was evidently slanting, and the cusp length measured was not its real length. The only reliable measurements would be the width of the posterior side and the width of the hook-body of the rachidian tooth and of the first 4-5 lateral teeth, a conclusion derived from observation of radular movement. When the odontophore is protruded, the cusps of the rachidian tooth and the several innermost lateral teeth are oriented anteriorly and the cusps of the outer lateral teeth are oriented anteriolaterally; in retraction the movement is reversed and all the cusps are again oriented posteriorly. The teeth in the median region move in the anterior-posterior direction with little or no rotation. Therefore, measurements in that region are exactly the same throughout radular movement.

Statistical analysis shows a positive correlation for all 4 populations between shell length (age) and number of lateral teeth, as well as shell length and number of rachidian teeth in the median longitudinal row. The width of the teeth also changes with the shell length (Table 2, Fig. 46). These observations, as well as the conclusions reached by Schutte & Van Eeden (1959), show the very limited value of radular formulae as taxonomic characters of freshwater pulmonates.

Though it is possible to distinguish these 4 cytologically distinct and geographically separated populations by radular morphology, we have seen above that there are similarities between populations I and III on the one hand, and populations II and IV on the other. The similarity is also reflected in the widths of the hook-bodies of the lateral teeth, which in populations II and IV are larger than in populations I and III in shell lengths between 3 and 9 mm (Table 2, Fig. 46). The radular similarities between populations I and III and populations II and IV reflect their closer relationships, which further supports similar speculations derived from the studies of shells and pigmentation of animals (greater globosity and lighter coloration in groups II and IV).

IV. Nervous System

According to Bargmann (1930), the nervous system of basommatophoran pulmonates can be divided into 2 types: (1) "basommatophoran" and (2) "zonitoid." The second type, which includes the left-handed freshwater pulmonate snails (Planorbidae, Physidae and Ancylidae), has a more concentrated visceral complex[9] than the first type, to which the right-handed snails, such as the Lymnaeidae, belong.

No morphological differences were found in the nervous system of the 4 populations. Hence, it has no value in the distinction of these species. Recent studies concerning the nervous system of the genus *Bulinus* are those of Demian (1960) on

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[7] B = distance between the tips of exocone and endocone; E = distance from the tip of the mesocone to the bottom on the gap between the mesocone and the exocone (cusp length).

[8] a, b = direct distance from the tip of mesocone to the gaps between either meso- and endocones or meso- and ectocones. Note that Schutte (1965) did not clearly define a and b in his paper.

[9] The "visceral complex" is comprised of 5 ganglia, i.e., 2 pleural, 2 parietal and 1 visceral or abdominal ganglion. Bargmann (1930) used "visceral ganglia" to denote these 5 ganglia. However, "visceral complex" is used in this text to avoid confusion with "visceral ganglion."

Bulinus truncatus, Stiglingh, *et al.* (1962) on *B. tropicus*, and Starmühlner (1969) on *B. liratus*. The present study agrees largely with that of Demian (1960) in the number of peripheral nerves and their courses of distribution. In general, exact comparison from the literature of peripheral nerves in the various species is not easy, because there is little agreement with regard to their terminology (see Table 13).

TABLE 13. Information available on the nervous system of genus *Bulinus* "s.s.".

References / Ganglion	This study *Bulinus* "s.s."	Demian (1960) *B. truncatus*	Stiglingh, *et al.* (1962) *B. tropicus*	Starmühlner (1969)* *B. liratus*
Cerebral	1 Ventrobuccal arterial n.	Not seen	"nerve to the wall of cephalic artery"	Not seen
	2 Sup. labial n.	Same**	Ant. labial n.	Int. labial n.
	3 Inf. labial n.	Same	Post labial n.	Med. or Ext. labial n.
	4 Penial n.	Same	Same	
	5 Optic-tentacular n.	Optic n. Tentacular n.	Ocular n. Same	Optic n. Same
	6 Statocyst n.	Same	Same	Same
Pedal	7 Ant. cervical n.	Same	Lateral n.	Propedial n.
	8 Post. cervical n.	Same	Lateral n.	
	9 Columellar n.	Same	Lateral n.	
	10 Ant. pedial n.	Same	Same	Metapedial n.
	11 Med. pedial n.	Central pedial n.	Med. pedial n.	
	12 Post. pedial n.	Same	Same	
	13 Parapedial n.	Not seen	Not seen	Not seen
Pleural	No peripheral nerve			
Rt. parietal	14 Rt. pallial n.	Same	Collar n.	Rt. pallial n.
Lt. parietal	15 Lt. pallial n.	Same	Osphradial n.	Lt. pallial n.
	16 Parietal n.	Ant. pallial n.	Lateral n.	"nerve to the mantle floor"
	17 Aortic n.	Same	Body wall n.	Aortic n.
Visceral	18 Splanchnic n.	Same	Uterine n.	Visceral or splanchnic n.
	19 Anal n.	Med.-Intern. pallial n.	Siphon, gill collar n.	Med. pallial n.
	20 Buccoretractor n.	Ventropallial n.	Buccal retractor n.	Int. pallial n.
Buccal	21 Esophageal n.	gastric n.	"Same as Watson (1925)"	"2 nerves to the pharyngeal muscles and 1 nerve to the salivary gland."
	22 Dorsobuccal n.	Salivary n.		
	23 Laterobuccal n.	Same		
	24 Ventrobuccal n.	Same		
	25 Postbuccal n.	Same		

*Names are translated from the Latin or German equivalents. Some of the finer nerves, though discussed in the text, are not shown in the diagrams.

**Same name as in column to the left.

V. Reproductive System

Except for the absence of the male copulatory organ in 5/6 of our *Bulinus truncatus* specimens, no significant morphological differences were found in the reproductive system of the 4 populations. The only differences were : (1) lack of uterine pouches in population II (*Bulinus truncatus*) and (2) the pear-shaped preputium probably due to partial protrusion of the penis into it, which consistently appeared in snails of population IV (*B. octoploidus*) with shells larger than 6 mm in length. The fact that uterine pouches were missing in the largely aphallic population II is interesting. Since during copulation the penis was observed to fill the whole uterus, with its tip reaching one of the uterine pouches (Fig. 77) in euphallic specimens, the loss of uterine pouches may well be coupled with the loss of the penial complex.

Although no significant morphological differences were found in the reproductive systems, there was a variation in the degree of development of the reproductive organs at corresponding shell sizes. The reproductive system of populations I and II in snails of 6 mm shell lengths (Figs. 80, a-b; 86, a-b) correspond well with those of 7.5 mm shell lengths of the higher polyploid populations III and IV (Figs. 94a-b; 99a-b). This difference in maturation is also expressed by the fact that snails of about 5-6 mm shell length already initiate spawn in populations I and II, while snails of populations III and IV never begin spawning unless they reach 7.5 mm or more in shell length.

The observed growth changes in the size of organs were interesting since the ovotestis was always the largest organ in young snails of less than 6 mm in shell length. Furthermore, at that size, male organs such as the prostate gland are always larger than female organs such as the albumen gland and spermatheca. As age increases, ovotestis and albumen gland become about equal in size. After the shell has reached a length of 7-8 mm the ovotestis remains more or less the same while the albumen gland rapidly increases its size and the spermatheca expands and becomes spherical. The later growth of the albumen gland and spermatheca in relation to the prostate is demonstrated by ratio changes during growth. The ratios given under "comparison of species" (p 126, 128) to illustrate the proportionately decreasing size of the prostate refer to the surfaces these organs occupy on drawings. Hence, figures for the volume ratio would have been much higher than the ratios given here. The earlier predominance of the prostate indicates that bulinine snails are characterized by protandrous hermaphroditism, which agrees with Wright's report on *Bulinus jousseaumei* (Wright, 1957).

The ratio of penial sheath to preputium has been used to define species by several workers (Mandahl-Barth, 1957, 1958, 1960; Wright, 1956, 1957, 1965, 1971; Brown, 1965, 1966; Schutte, 1966). However, there is considerable change in penial length associated with degree of maturation and growth, and there may be also size differences because various fixing fluids cause different degrees of shrinkage. Moreover, as Van Eeden (1958) pointed out, it is "not always possible, especially in the case of partly evaginated penis of *Bulinus* species, to locate with certainty the point of transition of penis sheath into praeputium." Hence, the practical taxonomic value of this character is questioned. Hubendick (1954) also stated that "Measurements of structures belonging to the genitalia are largely useless or even misleading unless the material is collected in such a way that the different sources of errors can be eliminated and the range of variation covered."

The majority of snails in population II were aphallic, a condition known to occur in the *truncatus* group. The percentage of aphallic snails is known to differ widely among different populations (Larambergue, 1939). The condition is a genetic character probably represented only in the genome of *Bulinus truncatus*, or species of the *truncatus* group, with the haploid chromosome number 36. Mandahl-Barth (1958) reported the occurrence of the aphallic condition in the following species or subspecies: *B. transversalis*, *truncatus*, *trigonus*, *rohlfsi*, *nyassanus* and *coulboisi*. For 3 of these, *B. truncatus*, *rohlfsi* and *coulboisi*, tetraploidy (n=36) has been cytologically determined (Burch, 1964; Lo, 1968); the chromosome number of the rest are unknown.

VI. Cross-breeding Experiments

From the results of cross-breeding 2 closely related and interfertile South African (Transvaal) populations of *Bulinus tropicus* (albino x population I), Crosses A and B, it is concluded that the genes for presence and absence of eye-pigment are 2 alleles at the same locus that are inherited in a Mendelian fashion in the expected ratio of 3 : 1 in the F_1 sibling matings, and in the ratio of 1 : 1 in the back-crosses of F_1 to the albino. The parental stocks of these 2 populations which can mutually cross-fertilize each other are separated by a distance of approximately 350 km.

In the crosses between the albino population and a population of *Bulinus natalensis* from Zululand, Natal, separated by a geographical distance of 520 km, Crosses C, D, E, fertilization proceeded only in one direction, from pigmented to albino snail. The albino parents were all able to produce eye-pigmented progeny, while the eye-pigmented snails failed to be cross-fertilized by their mates, since none of their descendants lacked eye-pigment (Table 6). Additional study of 2 shell characters, i.e., color (brown vs. white) and spire length (medium vs. low), revealed the general mode of inheritance of these characters: the albino population characteristic of brown shell color and medium spire length being dominant over the *B. natalensis* characters of white, high-spired shell. Since these shell characters were in various ratios in the F_1 and F_2 generations (Table 7), these 2 sets of characters were presumably polygenic in nature.

The experimental cross of albino (South Africa) and pigmented Ethiopian *Bulinus tropicus* (Crosses F, G, H, I) was designed to study whether and to what extent the crossing of normal diploids (n=18) from widely separated geographic regions (4,400 km) was possible. In 2 out of 4 crosses, albinos could be cross-fertilized to produce eye-pigmented F_1 progeny, though with a 25 and 28% embryo mortality. The other 2 albinos produced no, or non-embryonated, eggs. None of the eye-pigmented parents were fertilized by their albino mates. The direction of gene exchange was again in one direction, from eye-pigmented to albino snails.

That *Bulinus tropicus* from widely distributed regions can cross-fertilize to a certain extent, but with increasing difficulty as the geographical separation increases, agrees with the results of similar crosses with the related planorbid genus *Biomphalaria* (Paraense, 1956, 1959; Barbosa, *et al.*, 1956; Richards, 1962). However, in our case the cross could be made in one direction only (from pigmented to albino). The mechanism allowing the cross in one direction but preventing it in the other is unknown.

In the crosses between diploid albino and polyploid pigmented snails, when successful, only sterile progeny was produced. All such offspring had foot muscle esterase patterns showing a combination of the 2 parent characteristics (Figs.

104-106), indicating that crossing had actually occurred, although in only one direction, from albino to pigmented snail. The albino, unless self-fertilizing, never laid the egg masses,except a few that were non-embryonated. There may be some post-mating isolating mechanism, probably a gametic incompatibility.

Interestingly enough, diploid albinos, which did not cross with Egyptian tetraploids (*Bulinus truncatus*), did cross with Ethiopian tetraploids (*B. sericinus*) or octoploids (*B. octoploidus*), producing sterile progeny, though in only 1 out of 3 experiments with *B. sericinus* and 1 out of 4 experiments with *B. octoploidus*. However, when diploid albinos were crossed with hexaploids (*B. hexaploidus*), 4 out of 4 experiments succeeded in producing vigorous, but sterile, progeny. These facts indicate that the polyploid ova were compatible with diploid sperm, whereas the diploid ova were incompatible with the polyploid sperm.

Complete albinism is a double recessive character in these snails. One might expect that subsequent backcrossing of diploid-polyploid hybrids to the albino recessive would eventually produce polyploid albinos. In fact, such polyploid albino embryos did appear presumably in Experiment O a, b, (see p 145-146), but they lived, at most, only until hatching.

Although bulinine snails are hermaphroditic animals, the mode of fertilization, as a rule, is by cross-fertilization. When the mates were separated after actual mating had occurred, the snails at first exhibited the results of cross-fertilization, then there was a transitory period with both cross and self-fertilizated offspring, and finally there was a period of self-fertilization, presumably when the supply of allosperm was exhausted. The period of cross-fertilization varied from 2 to 9 weeks after isolation and the transitory period varied from 2 to 3 weeks. It is as though the switching from cross to self-fertilization depends on the quantity of allosperm received during copulation, and the quantity depends on the frequency and duration of copulation. Although cross-fertilization is dominant, some snails can also undergo partial self-fertilization (Table 4, Backcross c). Paraense (1956, 1959) reported that self-fertilizing *Biomphalaria* do shift to cross-fertilization after the introduction of a mate.

Defective egg masses (e.g., containing abnormal eggs of a creamy thread-like substance, or normal spawn with non-embryonated egg capsules), similar to those described for *Biomphalaria glabrata* (Paraense, 1959), were also observed in crosses from populations that were widely separated, as well as in eggs from old and senile snails. The impurity of the egg substance is a good indicator when one suspects the mixing of pure snail cultures in the laboratory.

VII. Systematics within *Bulinus* s.s.

Difficulties arise in grouping *Bulinus* "s.s." species on morphological grounds and, to some extent, on parasitological evidence. A good example for the inadequacy of these criteria, when used in absolute terms, are the 2 nominal taxa, *B. depressus* and *B. natalensis*, which both have a haploid chromosome number of 18 (*tropicus* group) but possess mesocones of variable, and of even angular (*truncatus*), type on the 1st lateral radular tooth (Schutte, 1965, 1966; Brown, *et al.*, 1967). At least 2 populations in this species complex are, moreover, somewhat susceptible to a strain of *Schistosoma haematobium* (Schutte, 1966; Lo, *et al.*, 1970).

There are 4 different chromosome numbers in *Bulinus* s.s.: those with the haploid chromosome number n=18 (normal diploid), n=36 (tetraploid), n=54 (hexaploid) and n=72 (octoploid) (Burch, 1967a). In immunocytological investigations (Burch & Lindsay, 1970), there was good correlation between *Bulinus* s.s. chromo-

some numbers and immunological characteristics. A species with any one particular haploid number, when tested with antiserum of a species with a different haploid number, always gave a "non-identity" reaction. Electrophoretically, 3 minor fractions of egg protein were demonstrated in the *truncatus* group, while in the other groups (*tropicus*, *africanus and forskalii*) only a single large fraction was present (Wright & Ross, 1965; Wright, 1971).

Evidence from the present study has demonstrated that in the polyploid series investigated there are: (1) almost no recognizable differences in the nervous and reproductive system, except slight differences in size, the higher polyploids being larger; (2) only slight differences in shell and radular morphology; (3) distinct differences in the pigmentation of the animals; (4) crosses among diploid populations (albino and pigmented) which were fertile and either mutual or in one direction only (from pigmented to albino snails); and (5) such diploid-polyploid crosses that did occur were one-directional (from albino to pigmented snails) and sterile. In practically all characters investigated, there were similarities between populations I and III and between populations II and IV.

Taxonomists as a rule do not give species recognition to populations that differ in chromosome number, unless they can be distinguished on the basis of external morphology. The frequent failure of diploid and polyploid individuals to successfully cross-mate, and the sterility of such progeny that did arise, indicate that isolating mechanisms exist and that there is a genetic discontinuity between them. Furthermore, immunological tests (Burch & Lindsay, 1970) demonstrated that these 4 populations are distinct. Hence, they seem to be genetically and biologically distinct species.

The higher polyploids in Ethiopia appear to occur only in the highlands (Brown & Burch, 1967; Burch, 1967a, b). The hexaploid snails occur mainly in the Sululuta River (24 km northwest of Addis Ababa on the Debra Markos Road) and the octoploid snails are found in several locations in Ethiopia (Brown & Burch, 1967; Lo personal communication) and West Aden Protectorate (Burch, 1964, 1967a, b; Natarajan, et al., 1965; Wright & Ross, 1965).

The finding of hexaploid and octoploid populations (Burch, 1964, 1967a, b; Brown & Burch, 1967) poses problems as to their relationships. Did these polyploids derive from one of the previously recognized extant species, and if so, from which, or was their origin so long ago that their relationships to present species is obscured? Do the polyploids themselves form a distinct taxon?

Both hexaploid and octoploid populations have so far been included in the *truncatus* group simply because (1) they are also polyploids, (2) the octoploid snails are also susceptible to *Schistosoma haematobium* (Lo, 1968), and (3) the octoploid snail of West Aden Protectorate has an electrophoretic egg protein pattern similar to that of the *truncatus* group (Wright & Ross, 1965). Evidence from this study in regard to shell characters, pigmentation of the animal, radular characters, and breeding experiments indicated that *Bulinus octoploidus* indeed belongs to the *truncatus* group, but that *B. hexaploidus* belongs to the *tropicus* group. Thus it would seem that the initiation of polyploidy from diploid progenitors probably occurred independently several times.

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BRIEF COMMUNICATIONS

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SEPTUM FORMATION IN THE FRESHWATER LIMPET *FERRISSIA WAUTIERI* (BASOMMATOPHORA: ANCYLIDAE) UNDER LABORATORY CONDITIONS.[1] — Amongst French Ancylidae, *Ferrissia wautieri* is the only species which is able to develop a septum, that is, a thin calcareous layer partially closing the shell aperture, which appears during the development of certain individuals in a population. The septum is therefore not a constant feature of the morphology of the species. It is thus fundamentally different from the calcareous shelf which limits the shell aperture of, for instance, *Crepidula*.

In *Ferrissia wautieri* all hatching juveniles are typical ancylids, but after hatching the development may proceed in 2 different ways. Either the individual grows and then reproduces without changing the shape of the shell, or the animal develops a septum before it starts to breed, then later forms a new shell from the edges of the constricted aperture. One following the first course retains throughout life the ancyloid shape; one following the second passes through 3 successive stages: ancyloid, septifer and post-septifer (Wautier, *et al.*, 1962).

Septum formation-rearing observations. Numerous observations during several years indicate that the presence of individuals with a septum is linked with conditions of the environment. We have therefore been led to study different rearing conditions. In some experiments we have thus obtained a relatively large number of individuals with a septum. The percentages of these, in such experiments, often reach values of between 50 and 75%, whereas in 9 years of monthly collections from a natural habitat (Montarcis pool, Commune de Taluyers, Rhone) the proportions of septifers and post-septifers combined have exceeded 50% only 5 times, these values generally remaining below 15%.

Nevertheless, the high percentages obtained in the laboratory derive from rearings for which the environmental conditions have been determined empirically; the results are not always reproducible. We are therefore still unable to define the precise conditions which favour development of septa.

In these rearings, when certain immature individuals have reached lengths of between 1.7 and 2.2 mm, growth ceases, the lateral borders of the shell become constricted inwards, towards its anterior third, whilst in front of this certain longitudinal ribs thicken and become very obvious. These 2 characters are signs that septum formation is about to begin. Its outline, in the form of a calcareous ridge, appears in the posterodextral angle of the shell, to which it is welded a little more deeply than the edge of the aperture.

The development of the septum begins posteriorly. It is completed when the septum has reached a length of 2/3 that of the shell. This hard, brittle layer is marked by growth striae which are concave anteriorly, and it bears a terminal thickening which forms a posterior border to the reduced shell aperture. The animal is then modified considerably, anatomically and physiologically (Wautier & Badarelli-Mille, 1966; Wautier, Hernandez & Richardot, 1966). The septifer stage, which persists as long as the environment is not modified, is characterised by a slowing down in metabolism.

Any renewal of the environment triggers off a resumption of growth around the new shell aperture, which produces an auricle-like shell of the characteristic post-septifer form. Such a resumption of growth may also interrupt the formation of a septum before it has reached its usual size. It then goes on around an aperture which is more or less reduced according to the degree of development of the calcareous layer. If the conditions of the environment change when the septum is in a rudimentary state, the shell of the animal retains an ancyloid appearance. Only a slight irregularity of the posterior surface of the shell reveals the presence of a septum interrupted in the course of construction (Fig. 1). Such post-septifer individuals, with an incomplete septum, have been obtained experimentally in the laboratory. We have also been able to obtain some such specimens from natural habitats.[2]

The return to a normal metabolism leads the individual to reproductive maturity. Deposition of the first batch of eggs completely prevents new septum formation, no matter what environmental conditions the animal may suffer subsequently. This is, moreover, equally true for animals which start reproduction in the ancyloid form.

The production of this calcareous layer therefore appears to be linked to a precise physiological state.

To sum up, it seems that septum formation intervenes when the individual is subjected to a conjunction of factors which fall into 2 categories, some being physiological in kind whilst the others are rather ecological.

Crystalline structure of the septum. Having as our first objective the study of the physiological mechanisms which determine the development of the septum, we thought it interesting to start by comparing its crystalline structure with that of the shell.

Material and methods. The empty, cleaned shells of 100 ancyloid individuals were ground up into a very fine powder.

From each septifer shell, the septum was excised under magnifying lenses. Only the central zone of the calcareous layer was selected, to avoid risk of including any fragments of shell. A powder was thus derived from the septa of 150 individuals. *X-ray diffraction*. The diffraction patterns of these 2 powders, placed in Lindeman tubes, were analysed in the Laboratoire de Minéralogie of the Université de Lyon

FIG. 1. Shell of a post-septifer individual with septum outlined (ventral view). S: Septum seen by transparency.

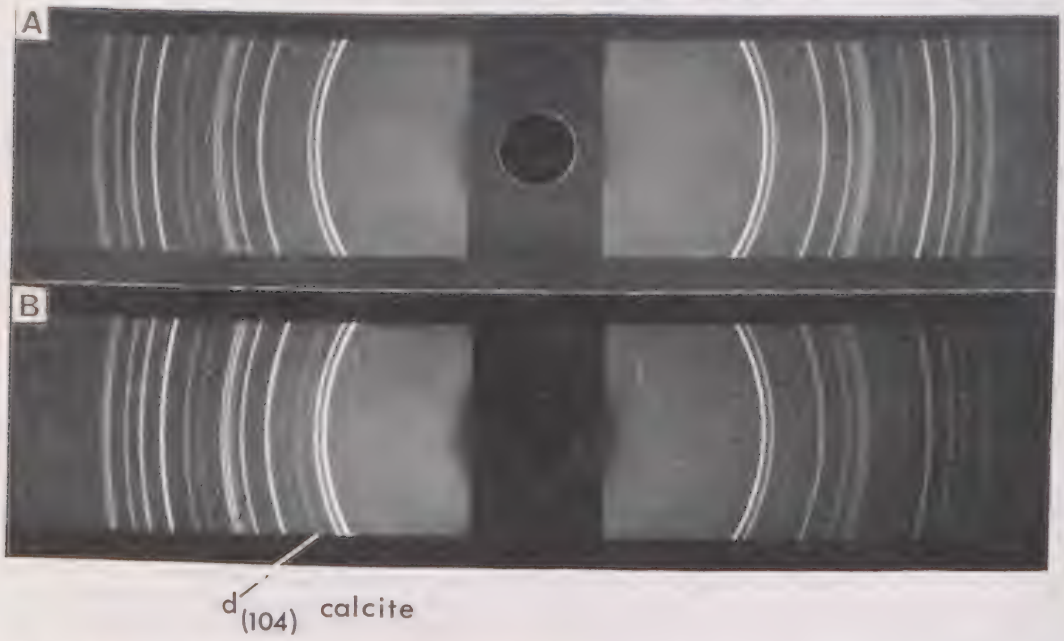

FIG. 2. Diffraction pattern of aragonite from (A) shell powder and (B) from septum powder. $d_{(104)}$ indicates the dominant line of calcite.

Claude Bernard, with a C.G.R. Theta 60 instrument, equipped with a Straumanis 360 mm camera and operating at 30 Kv with a copper target ($\lambda Cu_{K\alpha} = 1{,}5405$ Å).

Results. The 2 Debye-Scherrer patterns thus obtained, one with shell-powder (Fig. 2, A), the other with septum-powder (Fig. 2, B), reveal aragonite lines. Moreover, on both photographs, between the 2nd and 3rd aragonite line, it is possible to make out a very faint line corresponding to the dominant line of calcite ($d_{(104)}$: 3,035Å) (Fig. 2, B).

Thus in shell and septum alike, calcium carbonate is laid down as aragonite with a very faint trace of calcite. The presence together of these 2 crystalline forms is, moreover, not surprising. Reference to the work of Pobeguin (1954) shows that this phenomenon is very wide-spread in gastropods, with a general predominance of aragonite over calcite.

Conclusions. These results, therefore, provide evidence for a complete similarity in crystalline structure between shell and septum of *Ferrissia wautieri*. It seems possible to state that the septum is truly a part of the shell and to suppose, in consequence, that the formation of septum and of shell involves the same physiological mechanisms.

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(1) We are greatly indebted to Professor E. W. Knight-Jones for his translation of the manuscript.

(2) It is probable that one of the figures given by Burch (1964) for the species *Gundlachia* (*Kincaidilla*) *japonica* related to a similar post-septifer stage having an incomplete septum.

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THE SYSTEMATIC POSITION OF *"GUNDLACHIA (KINCAIDILLA) JAPONICA"* (BASOMMATOPHORA: ANCYLIDAE). — *Gundlachia (Kincaidilla) japonica* Burch 1964 is one of the 3 freshwater limpets that have been named from Japan. It belongs to a family of small to minute aquatic pulmonate gastropods that have received all too little attention. Literature relating specifically to Japanese Ancylidae is Kobelt (1879), Kuroda (1949), Inaba (1962, 1965), Burch (1964, 1965), Habe & Burch (1965) and Hubendick (1970). The latter study is a synopsis and revision of the Palearctic and Oriental species and "formgroups," and as such will undoubtedly be a very useful work. However, since its handling of the Japanese ancylids is rather confused, it seems appropriate to make some comments.

A brief recapping of the nomenclatural history of Japanese Ancylidae is as follows. Kobelt (1879) called his specimens collected at Kanga-Yashki in Yeddo (= Edo = Tokyo) by Hilgendorff *"Ancylus baconi* Bourguignat," an Indian species he considered to occur also in the Philippines and to be widely distributed throughout the Indian Ocean. Kuroda (1949) did not consider ancylid specimens from Kyoto, Japan to belong to this species, and so he named them as a new species, calling them *Protancylus (Laevapex) nipponicus*. The generic designation was later corrected to *Ferrissia* by Burch (1964, 1965) and Habe & Burch (1965). During our studies on Japanese ancylids which led to the latter publications, we noticed that in our collections there were 2 distinct and easily recognizable species, one corresponding to Kuroda's (1949) description and figure, as well as to his type specimens in the National Science Museum in Tokyo. The other species was described as *Ferrissia japonica* Habe & Burch 1965. A third Japanese ancylid, a septate form, was also described during this period as *Gundlachia (Kincaidilla) japonica* Burch 1964. But, the latter species was not assigned to the genus *Gundlachia* without some misgivings, the distinct possibility coming to mind that its septate shell might be merely a morphological expression of an unfavorable period of its environment. Because of that very possibility, the 2 most recently named Japanese species were both called *"japonica,"* i.e., should one go into the synonomy of the other, then there would not be a change in the specific name.

Hubendick (1970) recognizes *Gundlachia japonica* Burch to be distinct (as a *Ferrissia*), but considers *Ferrissia japonica* Habe & Burch to be the same as *F. nipponica* (Kuroda). However, I believe that if *F. japonica* is to be synonymized, it should be included with the species originally called *G. japonica*, not with *F. nipponica*. The reasons for this and a discussion of the genus *Gundlachia* are given in the following paragraphs.

The ancylid genus *Gundlachia* Pfeiffer 1849 traditionally has been considered to comprise those freshwater limpet-like basommatophoran snails possessing a septate shell, i.e., having a posterior shelf-like projection of shell material extending anteriorly, partially covering the shell aperture. The original specimens, from Cuba, on which Pfeiffer based both his new species (*G. ancyliformis*) and new genus (*Gundlachia*) were septate. However, it has long been suspected that the septate condition is not genetically determined (Dall, 1904, 1911), but ecologically conditioned, and more specifically, induced by drought conditions. And further, it has been surmised that the ecologically produced septate condition can occur in several different ancylid generic-group taxa (Basch, 1959). If that should be the case, then Pfeiffer's genus name would comprise a special group of normally non-septate (but occasionally septate) ancylids from Cuba, but perhaps having a wider distribution. Harry & Hubendick (1964) believe this to be the group represented by *"Ancylus" radiatus* Guilding, of which *G. ancyliformis* is a synonym. But, to whatever species group the original septate Cuban species of Pfeiffer belongs, it is somewhat unlikely that it belongs to the same group as the Japanese septate ancylids, which were previously called *Gundlachia (Kincaidilla) japonica*.

If the septum in freshwater ancylid snails is ecologically rather than genetically determined, and such ecological forms may occur in several different ancylid taxa, then *"Gundlachia" japonica* Burch 1964 would likely belong to the Australasian subgenus *Pettancylus* of the genus *Ferrissia*, as Hubendick contends, rather than to the Cuban true *Gundlachia* (assuming, of course, that the Japanese ancylids are consubgeneric with the Australian *"Ancylus" tasmanicus* Tenison-Woods 1876, the type species of Iredale's (1943) *Pettancylus*, used by Hubendick as a subgenus, and congeneric with the North American *"Ancylus" rivularis* Say 1819, type species of Walker's (1903) section *Ferrissia*). And, if the septate *"Gundlachia" japonica* Burch is conspecific with any other nominal Japanese species, then that species is undoubtedly *Ferrissia japonica* Habe & Burch 1965, not *F. nipponica* Kuroda as asserted by Hubendick. Thus, the specific designation with priority is *japonica* Burch 1964, and with the new name combination *Ferrissia (Pettancylus) japonica* (Burch 1964), *F. japonica* Habe & Burch 1965 would simply be a junior synonym.

With the exception of the septum, the shells of *Gundlachia japonica* Burch and *Ferrissia japonica* Habe & Burch are very similar. They are both low and elongate, and are both further characterized by radial ridges. *G. japonica* did not have the dense mantle pigment patches found on all of the populations of *F. japonica* we studied, but on the other hand, the formation of these pigment patches possibly may have been affected by the same environmental conditions causing the formation of the shell septum. (The variation in presence or absence of mantle pigmentation mentioned by Hubendick for *"F. nipponica"* is probably due mainly to the fact that his lot from the Botanical Garden of Kyoto University is a mixture of 2 different species, and to his mistaken interpretation of *F. nipponica* and *F. japonica*.) A much more basic similarity between *F. japonica* and *G. japonica* is their chromosome number, both having n=18 (Burch, 1965). Having the same chromosome number does not necessarily mean that the 2 species are conspecific. However, the fact that they do have the same chromosome number is perhaps more than a coincidence, since they are the only ancylid snails as yet known to have 18 pairs of chromosomes.

As mentioned above, I do not believe that *"Gundlachia" japonica* Burch can be synonomized with *Ferrissia nipponica* (Kuroda). In addition to the presence of a septum in the former (perhaps an ecologically induced structure), the shells of both are in other ways quite different. Hubendick is incorrect in saying

that *F. nipponica* has a more pronounced radial shell sculpture than *G. japonica*. In fact, just the reverse is true. *F. nipponica* is not only higher and more oval, but it does not have the radial raised ridges that are characteristic of *G. japonica* Burch and *F. japonica* Habe & Burch (see original species descriptions). Co-type material of *F. nipponica* in the National Science Museum (Tokyo), as shown to me by Dr. Tadashige Habe, fits Kuroda's original descriptions and figure. But an even more basic difference is found in the chromosome numbers. Whereas *G. japonica* Burch and *F. japonica* Habe & Burch both have 18 pairs of chromosomes, *F. nipponica* (Kuroda) has only 17 pairs (Inaba, 1965). Presumably this is a constant cytological difference between *F. nipponica* on the one hand and *G. japonica* and *F. japonica* on the other hand.

Finally, it would appear that Hubendick's figures of *Ferrissia nipponica* (Kuroda) (*sic* figs. 148-150, 160-164) and *F. japonica* Habe & Burch (*sic* figs. 154-159) are confused. Figs. 149, 154 and 158 seem to be *F. nipponica;* figs. 155-157, 159-164 apparently are *F. japonica*, as probably are also figs. 148 and 150. Additionally, it should be mentioned that the type locality of *F. japonica* Habe & Burch is Okoto, not Oboto.

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(1) Type locality of *Gundlachia* (*Kincaidilla*) *japonica:* pool at residence of Dr. Hiroshi Itagaki, 2-8-4 Taishido, Setagaya-ku, Tokyo, Japan. In 1964 and 1965 I was unable to get a more precise locality than "a pool at [Dr. Hiroshi Itagaki's] residence" in Tokyo. The more definite locality was given to me by Dr. Itagaki by personal communication when we met in Addis Ababa, Ethiopia in 1970. Dr. Itagaki also mentioned that septate forms had never been found in his pool since the original collection in 1963, perhaps a good indication that the septate condition is only an environmentally produced structure. The entire population apparently died about October 1968.

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MISCELLANEA

UNITAS MALACOLOGICA EUROPAEA

RESOLUTION

The *Unitas Malacologica Europaea*, representing malacologists and conchologists in Europe, is much concerned by the rapidly increasing destruction of the natural environment.

It therefore supports all measures being taken to avoid and reduce pollution.

Unitas Malacologica Europaea urges all who are concerned throughout the world to accept responsibility for ensuring the future existence of Mollusca and their habitats.

We, the members of *Unitas Malacologica Europaea*, realise that this will necessitate a curtailment of collecting activities, but we are sure that, as responsible naturalists, all conchologists and malacologists will wish to support appropriate conservation measures.

Unitas Malacologica Europaea therefore urges that for all purposes whatsoever only about the minimum number of specimens should be collected.

Observations as well as photography of living specimens in their natural habitats may be a much more rewarding activity than mere collecting. This applies equally to the work of the amateur and the professional.

Such an approach to field studies would result in the acquisition of much of the information which is so urgently needed to ensure the success of the efforts being made to conserve these animals. The European national malacological societies fully associate with this resolution and will publish it in their periodicals.

Dr. Oliver E. PAGET
Secretary

MALACOLOGICAL SOCIETIES' NEWS

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AMERICAN MALACOLOGICAL UNION. — The 38th annual meeting of the American Malacological Union took place at Galveston, Texas from July 9-14, 1971. Dr. Arthur S. Merrill of the National Marine Fisheries Service presided as President. The hosts were the shell clubs of Texas.

A number of interesting and valuable papers on malacology and related fields were presented, among them a series of 7 papers in a symposium on Genetics, Cytogenetics and Hybridization of Mollusks, with Dr. J. B. Burch of the University of Michigan as convener. The papers presented at this symposium were Cytogenetics of gastropod mollusks (C. M. Patterson), Oyster genetics and the probable future role of genetics in aquaculture (A. Crosby Longwell & S. S. Stiles), Hybridization in oysters (R. W. Menzel), *Oncomelania hupensis*: Hybridization, genetics and transmission of *Schistosoma japonicum* (George M. Davis), Genetics of *Biomphalaria glabrata* (Charles S. Richards), Cross-breeding experiments with the African snail genus *Bulinus* (Shi-Kuei Wu), and Development of hybrids between *Nassarius* species following experimental fertilization (James N. Cather, not presented formally). The Proceedings of the symposium will be published in *Malacological Review*, Vol. 6, No. 2.

A major address was given by Dr. Carol M. Lalli of McGill University at the final banquet, entitled "Unusual planktonic mollusks: The gymnosomatous pteropods."

Field trips were taken to Sabine Pass Beach and the coast near Freeport, as well as to selected land and freshwater collecting sites.

Abstracts of papers presented and a complete report of the meeting will appear in the next issue of the *American Malacological Union, Inc., Bulletin.*

The 38th meeting of the American Malacological Union will be held on June 24-29, 1973 at the University of Delaware, Newark, Delaware, under the presidency of Dr. Delores S. Dundee of Louisiana State University, who should be consulted for further details.

MOLLUSK SEMINAR, ANN ARBOR, AUGUST 1972. — A seminar on mollusks was held at The University of Michigan, Ann Arbor on 25 and 26 August 1972 to bring together researchers working toward common ends but using a variety of methods in studying mollusks. Two sessions were held, one on the first day and the other on the second. The first session, convened by Dr. George M. Davis of the Philadelphia Academy of Sciences, was on Multi-disciplinary Contributions to the Study of Systematics and Evolution of Mollusks. The second session, convened by Dr. C. M. Patterson of The University of Michigan, was a general session to include topics not covered by the first session.

Program

Opening remarks, J. B. BURCH

Multi-disciplinary Contributions to the Study of Systematics and Evolution of Mollusks.

Convener, George M. DAVIS

Integrated approaches to molluscan systematics. George M. DAVIS.
Some current research on the genus *Bulinus*. J. B. BURCH.
The systematic position of "*Stagnicola* (*Bakerilymnaea*) *cubensis*." P. T. LoVERDE and J. B. BURCH.
Electrophoretic techniques in malacology: applications and pitfalls. E. H. MICHELSON.
Electrophoretic variations in foot muscle esterases in populations of some African *Biomphalaria* species. F. M. A. UKOLI.
The occurrence of hemagglutinins in some Basommatophora and Stylommatophora. Paul RUDOLPH.
Pigmentation variations in *Biomphalaria glabrata* and other Planorbidae. C. S. RICHARDS.
Breeding experiments with *Stagnicola elodes* and *S. emarginata*. Patricia A. AYERS and J. B. BURCH
The podocyst in pulmonate evolution. J. N. CATHER.
Comparative observations on speciation in two species of prosobranchs, *Gibbula cineraria* (Linnê) (Trochidae) and *Littorina saxatilis* (Olivi) (Littorinidae). Jean M. GAILLARD.
Generic and specific taxonomic characters in succineid snails. C. M. PATTERSON.
Concluding remarks. George M. DAVIS.

General Session.

Convener, C. M. PATTERSON

Cytoplasmic localization in *Bithynia tentaculata* and its influence on development. N. H. VERDONK.
Ultrastructural development of *Ilyanassa*'s shell gland. Alex TOMPA.
Internal defense mechanisms of *Octopus dofleini*. C. J. BAYNE.
The role of galactogen in pulmonate snails. Esther M. GOUDSMIT.

Organic content of eggs and juveniles of an amphibious snail, *Pomacea urceus* (Müller), from the Venezuelan savannah and their ecological significance. Albert J. BURKY.

Activity patterns of the freshwater snail *Lymnaea stagnalis* (Say) exposed to sub-lethal elevated temperatures. Sharon C. McDONALD.

Reaction of pulmonate snails to temperature. Henry VAN DER SCHALIE and Elmer G. BERRY.

Apparent hybrids from a laboratory culture of *Lymnaea stagnalis* and *Bulimnea megasoma*. G. K. LINDSAY and J. B. BURCH.

Nominal *Physa* species in Michigan with a brief review of systematics of the Physidae. George A. TE.

Taxonomic problems in the Helisomatinae. G. L. PACE.

Bulinus sericinus from Ethiopia. S.-K. WU and J. B. BURCH.

Zoogeographical affinities between the naiad fauna of the Sydenham River, southwestern Ontario, and the Mississippi River basin. Carol B. STEIN.

On the distribution of Unionidae in the Sydenham River, southern Ontario. Arthur H. CLARKE.

Northern extensions of the Cumberlandian naiad fauna in tributaries of the Cumberland River in Kentucky. David H. STANSBERY.

Zoogeographical patterns in the marine bivalve fauna of the Canadian Arctic. Irene LUBINSKY.

A case for protecting the driftless area of the upper Midwest. Marc IMLAY.

Role of *Lymnaea stagnalis* (Say) and *Stagnicola reflexa* (Say) as intermediate hosts for *Plagiorchis noblei* Park, 1936. Harvey D. BLANKESPOOR.

Transmission of ostracods in snail aquaria. Y.-S. LIANG.

Incidence of a parasitic leech (*Marvinmeyeria* [=*Oculobdella*] *lucida* Moore) and two cercarial types in estivating *Stagnicola exilis* (Lea). Donald J. KLEMM.

BOOK REVIEWS

STUDIES IN TROPICAL AMERICAN MOLLUSKS. Bayer, Frederick M. & Voss, Gilbert L., editors. University of Miami Press, Coral Gables, Florida, U.S.A. 1971. 236 p, over 200 figs. US $12.50.

This volume consists of 4 papers with their abstracts and Spanish summaries, which were issued separately and previously in the *Bulletin of Marine Science*. Each deals with the results of the various biological expeditions of the Rosenstiel School of Marine and Atmospheric Science of the University of Miami. Two of them encompass reasonably circumscribed topics, namely, Voss' report on the cephalopods of the Gulf of Panama (p 1-34) and Nybakken's review of the Conidae of the same area (p 93-110). Olsson's naming and describing of various species of bivalves and gastropods from the Panamic Province of the Eastern Pacific (p 35-92) is redolent of another era, while Bayer's eclectic account of diverse clams and snails in the Caribbean region, though comparable, reflects more careful preparation.

The squids, octopuses and their relatives in Voss' paper number 26 species, 4 of which are new. Also, a new genus is established for a form which has "no representative or close ally in other regions of the world," a surprising statement in light of phylogeny. To the non-teuthologist, it seems risky business to describe 3 new species of the genus *Octopus* without adequate comparative or diagnostic comments separating them from the legions of other known species considered by Robson, and with *Octopus balboai* based on 1 male specimen and *O. stictochrus* on 2 female individuals. A résumé of previous work on the cephalopods of the region and a tabulation of the distributions of the species preface the systematic text.

Nybakken's short report summarizes what is known of the 11 species of *Conus* in the Gulf of Panama, with new data concerning their occurrence and distribution included, and with *C. poormani* Berry, a bi-nomen of dubious stature, illustrated for the first time.

Forty-one odd species of snails and clams from the Gulf of Panama are listed by Axel Olsson (p 35-92). Of the 15 new species introduced, most are uncritically and typologically described, most frequently on the basis of only single specimens, with inadequate, if any, comparison with related species. Acceptance of these nominal species may be questioned. Special remarks on the classification of the turrids, including some photomicrographs of radulae, are included, and the toxoglossate group is recognized at the family level, the Brachytomidae.

The final and major portion of the book (p 112-236) is a descriptive work on "new and unusual mollusks collected in the tropical western Atlantic." If the specimens had not been retrieved by the *Gerda* and *Pillsbury* and described by Bayer, one could easily mistake this for the work of Dall in the *Blake* or *Albatross* reports. Fifty-nine species, 4 bivalves and the remainder gastropods, are treated, of which there are several new taxa. Again it is disturbing to find so many new species described on single specimens; by my count, 10 new ones are established on only single specimens. However, at least, Bayer provides some remarks on these and contrasts them with known, related forms. Certain of the illustrations are excellent, including an elegant colored plate of living *Lyria cordis* and *Ficus howelli*.

Several interesting and important observations have been made: *Ficus atlantica* Clench & Aguayo is considered to be a junior synonym of *F. howelli* Clench & Aguayo. The species is sexually dimorphic with females having the color pattern of *atlantica*, the males with that of *howelli*. Ample evidence confirms the distinctness of the confusing species, *Murex cabritii* Bernardi, *M. donmoorei* Bullis and *M. olssoni* Vokes, the latter of which is now shown to be the most common and widespread shallow water muricid along the Caribbean coast of Panama and Colombia. The placement of *Dalium* Dall 1889 in the Oocorythidae is confirmed by the terminal nucleus in its operculum, similar to that of *Oocorys*, but unlike that of the cassids (e.g., *Sconsia* and *Morum*), which have a central or lateral nucleus. Two specimens are illustrated of the extremely rare *Bathygalea coronadoi* (Crosse), which were obtained at 280 meters depth off Isla Centinela, Venezuela, considerably extending the range of this species. A very unusual new genus and species of dimyid bivalve, *Basiliomya goreaui*, with a considerable distribution in the Bahamas and Jamaica, lives attached to scleractinian corals.

Such widely diverse papers scarcely deserve to be collected in a single volume, but for the financial supporters who have been instrumental in the cruises of the principal research vessels, *Gerda* and *John Elliott Pillsbury*, a bound volume represents a more tangible, solid contribution than scattered individual papers. Despite the high quality of the illustrations and the valuable geographic and systematic data, the inexcusable lack of an index seriously impairs the utility of the volume and is a disservice to those who will, nevertheless, have to use it.

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AUSTRALIAN SHELLS. Wilson, Barry R. & Gillett, Keith. Charles E. Tuttle Company, Inc. 1971. 168 p, 106 colored plates, 34 line cut or black and white figures, quarto. US $21.50.

Australian Shells is something of a misnomer, since the volume considers about 600 representative species of 34 prosobranch gastropod families. Along with Abbott's *American Seashells* and Habe & Kira's *Shells of the Western Pacific*, among others, it joins the ranks of quasi-scientific treatises aimed primarily at the amateur. With an emphasis on the groups most favored by amateurs, *Australian Shells* will nevertheless have to be welcomed by professionals, since it is the most extensive account of Australian prosobranchs available. It outdistances the more humbly produced, if not more critical (but geographically circumscribed), classics such as Cotton and Godfrey.

The introduction of about 20 pages instructs the reader about the diversity of the Phylum Mollusca, the untold richness of the Australian malacofauna (exaggeratedly assessed as "tens of thousands" of species), the varieties of the form, life, and manners of snails, and the zoogeographic regions and provinces of Australia. The authors acknowledge the singular provinciality which pervaded the earlier eras in the study of Australian mollusks, namely, the propensity of

workers to consider that fauna as distinct from the rest of the world and, consequently, to hamper critical work by overnaming the animals. For the most part, Wilson and Gillett conserve the more familiar generic names and bypass the plethora of unnecessary nomina invented by such enthusiasts as Tom Iredale. In sharp contrast to the broad generic taxonomy are the cumbersome systematics of Weaver and duPont, whose scheme the authors follow in their account of the Volutidae.

In the systematic portion of the text, each family is introduced by a remark on its diversity and biology, frequently accompanied by somewhat detailed comments on reproduction, behavior, ecology and bionomics. The usual treatment accorded each species is a description including an account of the shape, color, sculpture and size of the shell, at least one figure in color, a remark on the abundance and geographic range, and frequently a comment on related or synonymous forms. Nomenclatorially, generic, subgeneric, trivial, and even subspecific names are utilized in addition to the inclusion of the author and date of the original description. The use of *forma* names, for example among the highly variant cassid *Phalium pyrum* and the cypaeid *Zoila friendii*, is unfortunate, since they lack legal nomenclatorial status and will assuredly confuse the amateur. Additionally, the practice of enclosing the author's name and date in parentheses to signify that the specific nomen has been transferred to a genus other than that in which it was originally described (which is required by the International Code of Zoological Nomenclature, Article 51 d) has not been followed and will be annoying to the professional. However, the authors certainly are to be congratulated for not having succumbed to tempation: they do not invent common names for species.

The colored plates illustrating the various species usually have a grayish or bluish background and are frequently disappointing, since many individual shells appear out of focus. In marked contrast, the colored photographs of living specimens are beautifully reproduced, and on occasion, simply splendid. The authors acknowledge the fine photographs of Nelville Coleman and Don Byrne. Such plates as that of the volutes *Cymbiolacca wisemani*, *Amoria canaliculata* and *A. maculata*, which render and contrast the beautious colors of the living animal and its shell, are outstanding.

Particularly extensive attention is accorded families containing genera of especial interest to amateurs. The strombids, cypraeids, cassids, olivids and volutids are treated in much greater detail than such groups as the trochids, epitoniids, or littorinids, which receive cursory treatment. It is unfortunate that while over 60 species of cones and 70 cowries are listed, the highly diverse but small shelled turrids are not mentioned at all.

Only a few outright mistakes are evident (e.g., p 94, "Coralliophilidae and Harpidae (*sic*) are alternative names for the [Magilidae]"); but the book will certainly be helpful to the amateur and useful to the professional — even necessary to the reviser of the Harpidae since the holotype of *Austroharpa punctata* Verco 1906 is illustrated! A glossary defining the technical terms employed throughout the text, as well as an index to pages, plates and figures, enhances the utility of this volume.

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SHELLS OF JAPAN. Tadashige Habe, Translated by T. I. Elliott. Hoikusha Publishing Company, Osaka, Japan. 1971. 139 p.

A GUIDE TO SHELL COLLECTING IN THE KWAJALEIN ATOLL. F. B. Brost and R. D. Coale. Charles E. Tuttle Company, Rutland, Vermont, U.S.A. and Tokyo, Japan. 1971. 157 p. US $ 4.95.

INDEX NUDIBRANCHIA. Henry D. Russell. Delaware Museum of Natural History, Greenville, Delaware, U.S.A. 1971. 141 p. US $ 9.75.

Dr. Habe's small volume is a delight to amateur and professional alike. It is simply written and well translated so that each sentence carries a profundity which can only be captured by long experience and careful evaluation. The color illustrations are superb and the over-all production excellent. Most of all I liked the short discussions of Lake Biwa and its unique fauna and the discussion of the many ways the Japanese use mollusks.

The book on shell collecting in Kwajalein has one value. It gives specific collecting areas for many of the species found there. The illustrations are mediocre, the printing poor, and when one compares this book with Dr. Habe's, one has to wonder why the authors did not settle for a check list.

Henry Russell's catalog of the literature on nudibranchs from 1554 to 1965 is a volume of great service to malacologists, behaviorists and zoologists who want to know about nudibranchs. I checked the few references on development and found them accurate, complete and helpful. Even works with minimal coverage of nudibranchs are included. This is a work of fine scholarship.

JAMES N. CATHER

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The University of Michigan
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Malacological Review, 1972, 5: 177-196

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[1]Year for which the journal was first published.

[2]Prominent shell collectors' magazines may be included in future numbers of *Malacological Review*.

[3]Footnotes 4-23 list the main editorial offices of the various journals.

[4]18/55 Prince Albert St., Mosman, N.S.W. 2088, Australia.

[5]Senckenbergishchen Naturforeschende Gesellschaft, Senckenberg-Anlage 25, 6 Frankfurt 1, Germany (FR).

[6]The Nook, Uplands Rd., Bromborough, Cheshire, U.K.

[7]Delaware Museum of Natural History, Greenville, Delaware 19807, U.S.A.

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[9]National Science Museum, Ueno Park, Taito-ku, Tokyo, Japan.

[10]National Marine Fisheries Service, Oxford, Maryland 21654, U.S.A.

[11]3957 Marlow Court, Seaford, New York 11783, U.S.A.

[12]Rijksmuseum van Natuurlijke Histoire, Leiden, Netherlands.

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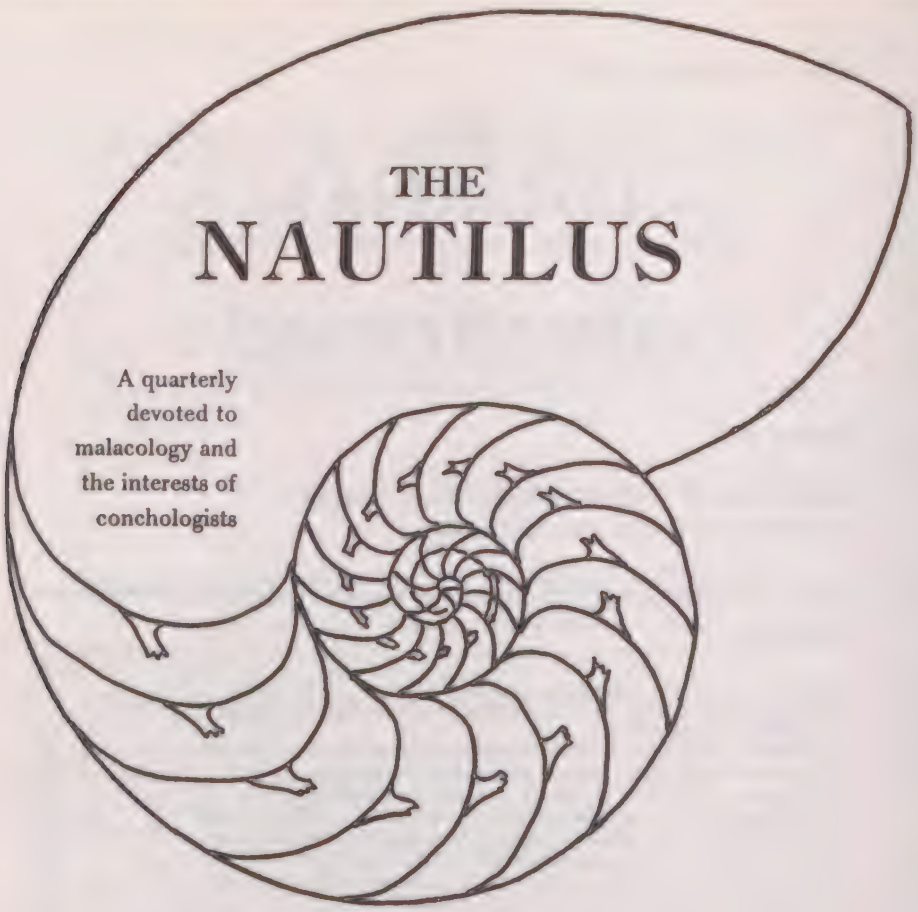

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